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# Bulletin

*of the*

# Torrey Botanical Club

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# New Rhodophyceae from Woods Hole[1]

CHIN-CHIH JAO

(WITH PLATES 10–13)

During the summers of 1933 and 1934, as the writer worked on both freshwater and marine algae of New England at the Marine Biological Laboratory, Woods Hole, Massachusetts, a number of new species were discovered. The freshwater forms have been reported under three titles in *Rhodora* and the *Transactions of the American Microscopical Society*. It is now proposed in this initial report to deal with species and records new to North America of the marine genera *Acrochaetium*, *Colaconema*, *Cruoriopsis* and *Erythropeltis*. This plants are all small forms, either epiphytic, endophytic, endozoic or epizoic. The members of *Acrochaetium* are most abundant between the tide marks or just below low tide on other red, brown or green algae, excepting *A. Alcyonidiae* and its variety *cylindricum* which were found on *Alcyonidium Mytili* washed on shore from rather deep water. The remaining genera were all deep water forms.

This study was made under the direction of Professor Wm. R. Taylor, University of Michigan, to whom the author is deeply grateful for his help and advice.

## ERYTHROPELTIS DISCIGERA Schmitz VAR. FLUSTRAE Batters

(Pl. 13, figs. 1, 2)

Fronds rose-colored, parenchymatous, of one cell layer, horizontally extended on the surface of the host, orbiculate, with irregular margin, up to 192$\mu$ in diameter; cells polygonal, oblong or irregular, irregularly arranged, 5–10 (–13)$\mu$ by 3–7 (–10)$\mu$; chromatophore single in each cell, parietal; gonidia globose, from 6 to 7$\mu$ in diameter, each being isolated from the vegetative cell by an oblique and curved wall.

This genus and species is new to North America. It is quite similar to the typical form as described by Batters, except that the gonidium is a little smaller. These plants were found on *Alcyonidium Mytili* Dalyell, washed on shore, Sheep Pen Harbor, Nonamesset Island, Woods Hole, Massachusetts, Sept. 1, 1934.

## **Colaconema americana**, sp. nov.

(Pl. 13, fig. 8)

Filamentis endophyticis, valde et irregulariter ramosis, fluenter innexibus inter cellulas corticales plantae matricis efficientibus; ramis lateralibus sparsis

[1] Papers from the Department of Botany and Herbarium of the University of Michigan, No. 548.

[THE BULLETIN FOR APRIL (63: 177–236) WAS ISSUED APRIL 1, 1936]

vel oppositis, sub angulo recto plerumque egredientibus, cellulis formo variis, plerumque in media valde tumidis, 5–10, interdum ad 32μ altis, 16–55, plerumque 22–38μ longis, membrana transversi 3–5μ altis; filamentis erectis extra corticali hospitis a filamentis endophyticis ramosis, multis et tenuis, longitudine 2–4- plerumque 3-cellularibus, apicem versus paulo attenuatis, cellulis forma cylindricis, cellulis basalis chromatophoro tenuiter evoluto, 3–5μ altis, 13–32μ longis, cellulis terminalibus hyalinis, solum 2.5–3.0μ altis; chromatophoris singulis, leviter lobatis, parietalibus, roseo-rubribus; monosporangiis sessilibus, frequenter in ramulis terminalibus lateralibus confertis, subglobosis, 9.6–13.0μ altis, vel in axis aut ramulis principalibus lateralibus solitariisque, forma depresso-globosis, subglobosis, lenticularibus vel hemisphaericis, 9.5–13.0μ latis, 6–13μ longis, raro in ramulis abbreviatis terminalibus; parte cellulae haud in monosporam mutata quasi operculum sporangii efficiente, crassitudine variabili, eiusdem genere vel leviter lamellose.

Endophytic filaments much and irregularly branched, interweaving between the cortical cells of the host plant; side branches arising from the main filaments or branches mostly nearly at right angles, scattered or opposite, cells varying in form, generally greatly tumid at intervals, 5–10 sometimes swollen up to 32μ diameter, 16–55, mostly 22–38μ long, cross walls 3–5μ diameter; from the endophytic filaments are produced the numerous, slender, and erect filaments free from the cortical layer of the host, 2 to 3, mostly 3 cells in length, their cells cylindrical in form, tapering toward the end, basal cells containing very poorly developed chromatophores, 3–5μ diameter and 13–32μ long, terminal cells colorless, only 2.5–3.0μ in diameter; chromatophore single in each cell, slightly lobed, parietal, rose-colored; monosporangia sessile, globose, often clustered on the short lateral branches, 9.6–13.0μ diameter, or solitary and lateral on the main filaments or branches, depressed-globose, subglobose, lenticular or hemispherical in form and 9.5–13.0μ diameter, 6–13μ long, rarely solitary and terminal on the short branches; monospore formed from part of the cell contents of the monosporangium, the remaining part forming a cup-like base below the monospore varying in thickness, and homogeneous or slightly lamellose.

The cup-like bases of the monosporangia are one of the quite remarkable characteristics of this genus. All the known species of this genus have the fronds entirely endophytic. This new species is separated from them by the presence of the distinct, numerous, short, erect and free hairlike filaments. Furthermore, it differs from *Colaconema Bonnemaisoniae* Batters in having larger vegetative cells and interwoven filaments, from *C. Asparagopsidis* Chemin in in having the monosporangia otherwise than strictly solitary and terminal on the branches, and the vegetative cells greatly tumid, from *C. Chylocladiae* Batters in not having the filaments united by lateral branches, by the vegetative cells being generally greatly swollen, and greater dimensions, and from *C. reticulatum* Batters, an in-

completely known species, in not having the fronds anastomosing, in never having side branches appressed to the main filaments or branches to form one filament with a double row of cells, and in having the length of the vegetative cells generally greater than the diameter.

This genus is one of the new records for North America. These new plants were found very abundantly in *Asparagopsis hamifera* (Hariot) Okamura from Gay Head, Marthas Vineyard, Massachusetts, July 17, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 272*.

**Acrochaetium unifilum,** sp. nov.

(Pl. 10, figs. 26–32)

Thallo minutissimo, epiphytico; cellula basali singula subhemisphaerica, filamenta erecta plerumque non ramosa, solitaria, rarissime bina, 1–9-cellula, a facie laterali cellulae basalis emergente, plus minusve curvata, plerumque ad hospitis superficiem parallela; cellulis vegetativis plus minusve tumidis, 6.5–13$\mu$ latis, 13–16$\mu$ longis; pilis plerumque pseudolateralibus, interdum terminalibus; chromatophoro stellari pyrenoideo centrali instructo; monosporangiis sessilibus, rarissime pediculo unicellulo, unilateribus, interdum 2 in cellulis singulis, ovatis, frequenter minoribus quam cellulis vegetativis, 5–6.4$\mu$ latis, 8–9.6$\mu$ longis; monosporiis liberis globosis, circa 7$\mu$ latis; articulo primo fili erecti exhibitum lateraliter a monospora germinate.

Plants very small, epiphytic, attached to the host by a single subhemispherical basal cell, giving rise to a single unbranched, 1- to 9-celled and erect filament from the lateral face, very rarely a second 1- to 3-celled short filament also arises from the same basal cell; filaments more or less arched, generally parallel to the surface of the host, about the same diameter throughout the whole plant; vegetative cells more or less tumid in the middle, 6.5–13$\mu$ diameter, 13–16$\mu$ long; hairs usually pseudolateral, sometimes terminal; chromatophore stellate, usually with four rays, with a central pyrenoid; monosporangia sessile, very rarely with a 1-celled pedicel, unilateral, sometimes two on each cell, oval in form, usually smaller than the vegetative cells, 5–6.4$\mu$ diameter, 8–9.6$\mu$ long; free monospores globose, about 7$\mu$ in diameter; when the monospore attaches to the host, it is gradually flattened on its attaching side and becomes hemispherical; the first articulation of the erect filament is laterally produced from the monospore and results in a single filament parallel to the host plant; sexual reproduction unknown.

These new plants are probably near to *Acrochaetium microscopicum* Naeg., but differ from it in having an unbranched erect filament arising from the basal cell laterally, the vegetative cells not bead-shaped, the hairs mostly pseudolateral and rarely terminal, and the monosporangia mostly only half the diameter of the vegetative cells.

Epiphytic on *Arthrocladia villosa* Duby, Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 274.*

**Acrochaetium microfilum,** sp. nov.

(Pl. 10, figs. 1–5)

Fronde minutissima, epiphytica, 40–60$\mu$ alta, 20–35$\mu$ longa (pilis exceptis); cellula basali solitaria globosa, maiore quam filamentae cellulis, circa 6.5$\mu$ diametro; fila plerumque 3, interdum 4, plana una sola et recta 2- vel 6-cellulares gignente; filis exterioribus plus extentis, directis vel paulo recurvatis, in hospite ferme decumbentibus; ramulis lateralibus vel dichotomis, cellulis doliiformibus, 3–5 (–6)$\mu$ latis, 3–5 (–6)$\mu$ longis; cellula terminali apicem versus sensim in pilum hyalinum attenuati; chromatophoro parietali, cellulam complenti vel paene complenti, pyrenoideo centrali instructo; monosporangiis regulariter secundis in filis aequis et secundis vel sparsis in filis erectis, plerumque sessilibus, rarius pediculo unicellulo, forma ovatis, 3–5$\mu$ altis, 6.5–8.0$\mu$ longis.

Plants epiphytic, very small, 40–60$\mu$ wide, 20–35 $\mu$ tall; basal cell single and globose, larger than the filament cells, about 6.5$\mu$ in diameter, with rather thick wall, from which are produced often three, sometimes four, free main filaments in a single vertical plane, 2–6 cells long, the outside two filaments more extended, straight or slightly arched downward, almost decumbent on the host, the remaining filament or filaments erect, branches lateral or dichotomous, cells barrel-shaped, 3–5 (–6)$\mu$ diameter, 3–5(–6)$\mu$ long; the terminal cell tapering toward the end to form a hyaline hair; chromatophore parietal, filling or nearly filling the cell, with a central pyrenoid; monosporangia regularly secund on the horizontal filaments, secund or scattered on the erect filaments, mostly sessile, rarely with one-celled stalks, oval in form, 3–5$\mu$ diameter, 6.5–8.0$\mu$ long.

This species should be compared with *Acrochaetium crassipes* Børgesen, *A. trifilum* Batters, *A. parvulum* (Kylin) Hoyt and *A. pulchellum* Børgesen, but it differs from the first in having the chromatophores not stellate, and a globose basal cell; from the second in not having the monosporangia globose; from the third in never having the monosporangia opposite in arrangement; from the fourth in having the basal cell undivided, the filament not creeping on the host, but in a regular fan-shaped arrangement; and from all of them in having smaller dimensions of all cells.

Found on *Polysiphonia fibrillosa* together with several other species of *Acrochaetium*, Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 274.*

**Acrochaetium compactum,** sp. nov.

(Pl. 10, figs. 6–14)

Thallo epiphytico, minutissimo, 22–42$\mu$ longo et 38–61$\mu$ alto (pilis exceptis); cellula basli singula globosa vel subglobosa, membrana crassa, plerumque grandiore quam filamentarum cellulis, circiter 8–10$\mu$ alta; filis erectis plerumque 3, interdum 2 vel 4, a cellula basali ramosis, valde expandis, plus minusve irregulariter ramosis, ramulis brevibus plantarum nitidarum frequenter fasciculatis, apicem versus sensim paulum attenuatis, cellulis doliiformibus, 5–8$\mu$ altis, 5–10$\mu$ longis; pilis terminalibus; chromatophoro stellaeformi, pyrenoideo centrali instructo; monosporangiis sessilibus, terminalibus, secundis vel sparsis, raro oppositis, 1 vel 2 in articulis singulis, ovatis vel subglobosis, 5.0–6.5$\mu$ altis, 6.5–7.0$\mu$ longis.

Plants epiphytic, very small, 22–42$\mu$ tall and 38–61$\mu$ broad (except hairs); basal cell single, globose or subglobose, with a thick wall, especially on the lower side, generally larger than the filament cells, 8–10$\mu$ diameter, from which are produced mostly three, sometimes two or four erect main filaments more expanded in a single plane, more or less irregularly branched, branchlets of the well developed plants frequently tufted, gradually slightly tapering toward the end, cells barrel-shaped, 5–8$\mu$ diameter, 5–10$\mu$ long; hairs terminal; chromatophore stellate, with a central pyrenoid; monosporangia sessile, terminal, secund or scattered, rarely opposite, mostly 1, sometimes 2, on each articulation, ovate or subglobose, 5.0–6.5$\mu$ diameter and 6.5–7.0$\mu$ long.

These plants are related to *Acrochaetium moniliforme* (Rosenvinge) Børgesen and *A. crassipes* Børgesen, but differ from the first in having lesser dimensions of all cells and the branchlets tufted in well developed plants, and from the second in having the filaments often more than two, the basal cell globose in form, and the branchlets tufted.

Very abundant on *Cladophora* sp. from Black Rock, Sconticut Neck near Fairhaven, New Bedford, July 25, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 275.*

**Acrochaetium moniliforme** (Rosenvinge) Børgesen
var. **Mesogloiae,** var. nov.

(Pl. 10, figs. 15–17)

Thallo minuto, epiphytico, 40–90$\mu$ alto et 40–65$\mu$ longo (pilis exceptis); cellula basali singula subglobosa vel subovata, 8.0–9.6$\mu$ lata, 11–17$\mu$ longa, membrana basali crassitudine usque ad 3.5–5.0$\mu$ et plus minusve distincte lamellosa, forma subhemisphaerica, intra membranum gelatinosum immerse et cellulum circumdatum hospitis adjuncto; fila plerumque 1, rarissime 2 vel 3, plus minusve recurvata; thallo unifilamentio plerumque 1 vel 2 ramulis ex cellula prima fili, plus minusve dichotomis vel interdum oppositis, apicem versus sensim paulum attenuatis, cellulis apiceis 6.5$\mu$ latis, 9.6$\mu$ (pilis exceptis)

longis, cellulis reliquis 8.0–9.5$\mu$ latis, 6.5–9.6$\mu$ longis, doliiformibus, membrana tenui; pilis terminalibus, stabilibus, 1 vel 2 in omnis cellulis terminalibus; chromatophoro stellaeformi, pyrenoideo centrali instructo; monosporangiis ovatis, 6.5–8.0$\mu$ latis, 9.5–16.0$\mu$ longis, plerumque sessilibus, interdum pediculo unicellulo, saepe in articulorum singulorum parte superiore secundis, raro oppositis.

Plants minute, epiphytic, 40–90$\mu$ wide, 40–65$\mu$ tall; basal cell subglobose to subobovoid, 8.0–9.6$\mu$ diameter; 11–17$\mu$ long, with a subhemispherical basal wall up to 3.5–5.0$\mu$ thick, more or less distinctly lamellose, immersed in the mucilage layer and attached to the peripheral cells of the host; from the basal cell producing mostly 1, very rarely 2–3 main filaments, more or less recurved; in the single filament type, generally one or two strong branches arise from the first cell of the main filament, branches few, as thick as the main filament, more or less dichotomous in form, or sometimes opposite, gradually a little tapering toward the end, tip cells about 6.5$\mu$ diameter and 9.6$\mu$ long (except hairs), the other cells 8.0–9.5$\mu$ diameter, 6.5–9.5$\mu$ long, barrel-shaped, cell wall thin; hairs present in all stages, thick, basal parts 3.0–3.5$\mu$ diameter, up to 120$\mu$ long, one or two terminal on the tip cell; chromatophore stellate, with a central pyrenoid; monosporangia oval, 6.5–8.0$\mu$ diameter, 9.5–16$\mu$ long, mostly sessile, occasionally with a 1-celled stalk, often secund on the upper side of each articulation, rarely opposite.

This variety differs from the typical species in having the main filament usually single, the main branches arising from the cell adjoining the basal cell, which is greatly thickened on the lower side; the thick hairs occurred in all stages, and the ramification was mostly dichotomous.

Plants found on *Mesogloia divaricata* (Ag.) Kütz., Sheep Pen Harbor, Nonamesset Island, in the Elizabeth Island chain off Woods Hole, Massachusetts. Type in C.-C. Jao collection and Herb. Univ. Mich., *Woods Hole No. 276*.

**Acrochaetium intermedium,** sp. nov.

(Pl. 11, figs. 1–4)

Thallo endophytico, 1–2 mm. alto, cellulis basalibus elongatis, 13–16$\mu$ altis, 32–57$\mu$ longis, 1–3 filis rhizoideis gignentibus, longitudine 1- vel 5-cellularibus; parte inferiore cellulae basalis et filis rhizoideis in vel inter membranum hospitis penetratis; filamentis erectis singulis, a basi ramosis, ramulis secundariis regulariter secundis, cellulis 8–10$\mu$ altis, (26–) 32–64$\mu$ longis; cellula terminali leviter attenuati, crassitudine circa 6.5$\mu$; chromatophoro parietali pyrenoideo centrali instructo; sine pilis; bisporangiis et monosporangiis cylindrico-obovoideis vel ovatis, 9–13$\mu$ altis, 19–23$\mu$ longis, plerumque sessilibus, rarius pediculo unicellulo, in cellulis ramulorum inferioribus secundis, 2- 6-seriatis, interdum unilateraliter sparsis in parte superiore filorum principium, cellula inferiore plerumque longiore quam superiore.

Plants endophytic, 1–2 mm. tall; the base consisting of the original spore, which elongates downward to form a cuneate prolongation, penetrating into the host plant between or in the cell walls, from the basal cell, or rarely from the adjoining cell, giving rise to one to three rhizoidial filaments of 1–5 cells in length, wholly imbedded in cell walls of the host plant, except those rhizoids which rise from the adjoining cell, the upper part of the basal cell retaining the original spore form, 13–16$\mu$ in diameter, but elongated to 32–57$\mu$; from each spore a single erect main filament arises, ramifying by numerous long branches beginning near the basal cell; secondary branches regularly secund, cells 8–10$\mu$ diameter, (26–) 32–64$\mu$ long, terminal cells tapering, with a diameter about 6.5$\mu$; chromatophore parietal, a little lobed on both ends, generally occupying the upper end of the cell, with a prominent central pyrenoid; hairs absent; bisporangia and monosporangia cylindric-ovate to ovate, 9–13$\mu$ diameter, 19–23$\mu$ long, secund, mostly sessile, rarely 1-celled pedicellate, placed upon the lowermost cells of the branches or branchlets, two to six on each branch, occasionally also scattered unilaterally on the upper part of the main filaments; the upper cell of the bisporangium is generally shorter than the lower.

The writer's materials are rather past their full maturity. The upper cells of the bisporangia are mostly empty and only a few bisporangia were found containing spores in both upper and lower cells. The empty bisporangia were commonly divided by a very clear, straight cross wall, especially when placed upon the lowest articulations of the branches.

These plants have some characteristics of both *Acrochaetium Dasyae* Collins and *A. opetigerum* Børgesen, but differ from the first in having an endophytic base, an elongated basal cell (original spore) often with rhizoidial filaments penetrating into the cell wall of the host, greater dimensions of all cells, and much more abundant branching; from the second in having the secondary branches regularly secund; and from both in having the sporangia quite often divided into two cells.

The plants are abundant and mostly grow at the fork of the pinnules of the host plants, *Dasya pedicellata* C. Ag., rarely on other parts. Collected from Grassy and Pine Islands, Woods Hole, Massachusetts, Aug. 7, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 277*.

**Acrochaetium subseriatum,** sp. nov.

(Pl. 11, figs. 5–7)

Thallo epiphytico, cellula basali elongata, membrana crassa, filis repentibus depravatis e cellula basali et cellula adjacentia ramosis; filum erectum a spora mutabili orientem, altitudine usque ad 2–3 mm., a basi magna parte ramosis, ramis inferioribus valde longioribus quam superioribus; ramis secundariis crebris, secundis vel alternis; cellulis 6.4–9.6$\mu$ altis, 32–70$\mu$ longis;

pilis terminalibus, rarissimis; chromatophoro parietali pyrenoideo centrali instructo; monosporangiis sessilibus vel pediculo unicellulo, secundis prope basim ramorum, raro sparsis, cylindrico-ovatis, 6.5–9.5$\mu$ altis, 22–31$\mu$ longis.

Plants epiphytic; basal cell elongate, with a thick wall, with the adjoining cell giving rise to contorted creeping filaments; solitary erect main filament arising from the modified spore cell, up to 2–3 mm. tall, freely branched, the lowest branches quite near the base, much longer than the upper ones, gradually shorter upward, branchlets very numerous, secund or alternate, cells 6.4–9.6$\mu$ diameter, 32–70$\mu$ long; hairs terminal, very rare; chromatophore parietal, containing a central pyrenoid; monosporangia mostly borne on each articulation of the branchlets, sessile or with 1-celled stalks, secund near the base of the branchlets, rarely scattered, cylindric-obovoid in form, 6.5–9.5$\mu$ diameter, 22–31$\mu$ long.

These plants are related to *Acrochaetium seriatum* Børgesen and *A. Sagraeanum* (Mont.) Bornet, but differentiated from both in that erect filaments do not arise from the creeping filaments, and the cylindric-obovoid monosporangia are much longer. The basal part of *A. seriatum* Børgesen consists of short, irregularly bent, creeping filaments, fusing together in the middle into a small disc. In *A. Sagraeanum* (Mont.) Bornet the basal layer is composed of contorted and entangled filaments, from which the erect filaments arise.

Plants epiphytic on *Zostera*, mixed with *Acrochaetium virgatulum* var. *luxurians*. Collected from Nobska Point, Woods Hole, Massachusetts, Aug. 25, 1933. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 278*.

### Acrochaetium attenuatum (Rosenvinge) Hamel 1927
(Pl. 12, fig. 1)

Plants epiphytic; basal filaments fused together near the center to form a 1-layered disc, ramification mostly dichotomous or opposite, irregularly extended from the center, cells 6.5–9.5$\mu$ diameter, 6.5–11$\mu$ long; erect filaments numerous, arising from the central part of the basal disc, up to 250 (or more)$\mu$ tall, ramification scattered, opposite or dichotomous, the terminal cells tapering toward the tip and forming a terminal hyaline hair, cells 5.0–6.5$\mu$ diameter, (6.5–) 9.5–16$\mu$ long; chromatophore parietal, with a prominent pyrenoid; monosporangia occur mostly on the upper part of the plant and usually are solitary, mostly sessile, sometimes with a 1-celled stalk, oval in form, 4.0–6.5$\mu$ diameter, 6.5–9.6$\mu$ long.

These plants as described above seem to be very close to *Acrochaetium attenuatum* (Rosenvinge) Hamel, except that the erect filaments are shorter and hairs do not disappear on the longest filaments. Probably the writer's samples are in a rather young condition, but the growth habit and measure-

ments are quite in accord. This species is newly recorded for North America.

Found on *Polysiphonia fibrillosa* together with several other species of *Acrochaetium*, Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934.

**Acrochaetium Alcyonidiae,** sp. nov.

(Pl. 12, figs. 2–4)

Filamentis basalibus endozoicis, valde longioribus quam filamentis erectis, intra hospitem penetratis, raro partibus epizoicis, abunde at plerumque dichotomiter ramosis, cellulis plerumque medio tumidis, 6.5–13$\mu$ latis, 13–32$\mu$ longis; filamentis erectis usque ad 600$\mu$ altis; ramulis plerumque 1- 5-, interdum ad 10-, cellularibus, brevissimis, secundis vel sparsis, cellulis 6.5–9.5$\mu$ latis, 9.5–19$\mu$ longis; sine pilis; chromatophoro parietali, pyrenoideo centrali instructo; monosporangiis obovoideis, sessilibus vel pediculo unicellulo, 1 vel 2 in ramulorum articulis singulis, terminalibus vel secundis, plerumque dense confertis, 8.0–9.5$\mu$ latis, (13-) 16–19$\mu$ longis, interdum bisporangiis repositis.

Plants endozoic below, the basal filaments much longer than the erect filaments, deeply penetrating into the host between the individuals of the colony, rarely a part of them epizoic, abundantly and usually dichotomously branched, the cells varying in size and shape, 6.5–13$\mu$ diameter, 13–32$\mu$ long, often swollen in the middle; the free filaments erect, up to 600$\mu$ long, with very short branches, which are usually 1–5, sometimes up to 10 cells long, secund or scattered, cells 6.5–9.5$\mu$ diameter, 9.5–19$\mu$ long; hairs absent, occasionally the terminal cells gradually much tapered toward the end, but containing chromatophores; chromatophore single, parietal, with a prominent central pyrenoid; monosporangia obovoid, sessile or with a 1-cell stalk, 1 or 2 on each articulation, terminal or secund, very rarely otherwise, in crowded groups on short branches, 8.0–9.5$\mu$ diameter, (13–) 16–19$\mu$ long; occasionally replaced by bisporangia.

This species differs from *Acrochaetium Daviesii* (Dillwyn) Naegeli in having a strongly marked endozoic habit and very short lateral branches. In size and habit it is near to *Acrochaetium endozoicum* (Darbishire) Hamel, but *A. endozoicum* has shorter free filaments with copiously forked branches as shown in Darbishire's drawings, and much shorter monosporangia.

Found on *Alcyonidium Mytili* Dalyell, washed ashore in Sheep Pen Harbor, Sept. 1, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 279*.

**Acrochaetium Alcyonidiae** Jao var. **cylindricum,** var. nov.

(Pl. 12, fig. 5)

Filamentis endozoicis 5.0–6.5$\mu$ latis, cellulis 6.5–13$\mu$ longis; filamentis erectis ad 300$\mu$ altis, cellulis 4–5$\mu$ latis, 10–19$\mu$ longis; ramulis lateralibus

brevissimis, longitudine 1–4-cellulis; monosporangiis cylindrico-obovoideis, plerumque terminalibus, raro lateralibus, 4.0–6.5$\mu$ latis, 9.5–13$\mu$ longis; ceterum forma typica similis.

Endozoic filaments 5.0–6.5$\mu$ diameter, the cells 6.5–13$\mu$ long; erect filaments up to 300$\mu$ tall, cells 4–5$\mu$ diameter, 10–19$\mu$ long; branches very short 1–4 cells long; monosporangia cylindric-obovoid, usually terminal, rarely lateral, 4.0–6.5$\mu$ diameter, 9.5–13$\mu$ long; otherwise as in the type species.

This variety differs from the type form of the species in having all cells of lesser dimensions and the cylindric-obovoid monosporangia mostly terminal on the very short branches. It also bears some resemblance to *A. strictum* (Rosenvinge) Hamel and *A. gracile* Børgesen, but differs from both in having an endozoic habit; furthermore, the first has greater dimensions of all cells, the branches are longer and hairs are present, and the second has filaments with long branches which taper toward the tip and often end in long hair-like prolongations, and has larger sporangia.

Growing on *Alcyonidium Mytili* Dalyell mixed with *Acrochaetium Alcyonidiae* Jao, and partly endozoic, washed ashore in Sheep Pen Harbor, Sept. 1, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 279: B.*

**Acrochaetium radiatum,** sp. nov.

(Pl. 10, figs. 18–25)

Thallo epiphytico, prostrato, ferme orbiculato vel irregulare, altitudine ad 320$\mu$; spora germinante in duas cellulas plus minusve aequales divisa, ex quibus 3–6 (raro ultra) fila ramosa repentes procreantibus, plus minusve radiatis compositibus; filis abunde ramosis, ramulis ad media pars thalli plerumque oppositis et dense compositis, forma pseudo-parenchymaticis, ramulis ad apicem filiorum plerumque furcatis vel secundis et fluxis; cellulis 5.0–6.5$\mu$ altis, 6.5–9.5$\mu$ longis; ramulis erectis non visis vel tenuiter procreantibus, solum 1- vel 3-cellularibus; chromatophoro parietali, pyrenoideo centrali; pilis terminalibus, plerumque in filis erectis; monosporangiis in filis prostratis, singulis et sessilibus, raro 1 vel 2 in filis erectis terminalibus, ovatis, (5–) 6.5–8.0$\mu$ altis, 8.0–9.5$\mu$ longis.

Plants epiphytic, prostrate on the host, almost circular in form or irregular, up to 320$\mu$ broad; the germinating spore dividing into two nearly equal cells, from which are produced 3–6 (or rarely more) main filaments in all directions in a single plane, resulting in a more or less regularly radiate arrangement of the filaments; abundantly branched, the branches near the center usually opposite and densely arranged, resulting in a pseudo-parenchymatous appearance, the branches near the end of the main filaments often dichotomous or secund and loose, their cells 5.0–6.5$\mu$ diameter, 6.5–9.5$\mu$ long; erect branches absent or poorly developed, only 1–3 cells long; chromatophore parietal, with a central pyrenoid; hairs terminal, mostly on erect filaments;

monosporangia directly produced on the prostrate filaments, or sometimes 1 or 2 terminal on the erect branches, oval in form, (5–) 6.5–8.0μ diameter, 8.0–9.5μ long.

These plants bear some characteristics of *Acrochaetium reductum* (Rosenvinge) Hamel, *A. humile* (Rosenvinge) Børgesen and *A. pulchellum* Børgesen, but differ from them chiefly in having more than two main filaments arising from the divided germinating spore and all the filaments arranged radiately and densely from the center of a fully developed thallus. Beside these characteristics, this new species is separated from the last two especially by the absence of stellate chromatophores. *Acrochaetium maculum* (Rosenvinge) Hamel also has a circular frond which is composed of more or less regularly radiating filaments and is pseudo-parenchymatous in appearance, but it has stellate chromatophores and a different method of spore germination.

Found on *Polysiphonia fibrillosa* Grev., together with several other species of *Acrochaetium*, Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 280.*

### Acrochaetium emergens (Rosenvinge) Hamel
(Pl. 13, figs. 7, 7B)

Vegetative filaments wholly endophytic in the cuticular layer of the host plant, horizontally extended; branches generally given off from the main filaments at right angles; cells varying in shape, mostly swollen in the middle, 1.5–3.5μ diameter, 9.5–12.8μ long; chromatophore parietal, occupying a large part or filling the cell, pyrenoid apparently absent; monospores terminal on a 1-cell stalk, and entirely free from the host, or sessile and endophytic, oval in form, 3.2μ diameter, 4.5–5μ long.

This local form is quite similar to Rosenvinge's type, except for a little difference in size. It is a new record for North America, and was found in *Polysiphonia fibrillosa*, from Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934.

### **Cruoriopsis Ensisae,** sp. nov.
(Pl. 13, figs. 3–6)

Thallo horizontaliter expando, lineamento irregulari, usque ad 3 mm. diametro, strato basali monotromatico e filis radiantibus approximatibus composito, crassitudine 13–19μ; ramulis dichotomis, cellulis aspectu superficiali quadrangulatis vel oblongis, raro triangulatibus, (3.2–) 6–11μ latis, 6–16μ longis; per temporam fructiferam filamentis erectis basi dispositis procreantibus, longitudine 2- vel 4-cellularibus, cellulis 6.5–9.5 altis, 9.5–13μ longis; chromatophoris nonnullis continentibus, colore roseo, parietalibus, disciformi-

bus; tetrasporangiis in filis erectis 1-cellularibus terminalibus, inter filas sterilias, ovatis, 16–25$\mu$ altis, 22–35$\mu$ longis, irregulariter cruciatim divisis; partes sexuales ignoti.

Fronds horizontally expanded, irregular in outline, up to 3 mm. in diameter, 13–19$\mu$ thick; filaments mostly dichotomously branched, appressed to each other to form the basal layer; cells square or oblong, rarely triangular in surface view, (3.2–) 6–11$\mu$ diameter, 6–16$\mu$ long; during the fruiting stages the erect filaments two or four cells long arise from the basal layer in groups, their cells 6.5–9.5$\mu$ diameter, 9.5–13$\mu$ long; several rose-colored parietal disc-shaped chromatophores in each cell; tetrasporangia produced among the free filaments, on stalks of one cell, ovate, 16–25$\mu$ diameter, 25–32$\mu$ long, irregularly cruciate divided to form the tetraspores; sexual reproduction unknown.

It is unfortunate that the sexual organs of this species were not found in the writer's collections. His determination was based upon the tetrasporangial plants, which showed the characteristic encrusting monostromatic basal layer and the irregularly cruciate tetrasporangia terminal on short stalks between the sterile erect filaments, which are features quite similar to the genus *Cruoriopsis*, but these plants differ from the type and other species of that genus in having the erect filaments in groups on the basal disc and the cells containing several disc-shaped chromatophores. This terminal tetrasporangium is also found in the genus *Rhododiscus*, but all the erect filaments of *Rhododiscus* are terminated by the tetrasporangia, *i.e.*, sterile erect filaments are absent. *Cruoriopsis hyperborea* Rosenvinge reported from Ellesmere Land has thicker crusts, longer sterile erect filaments and much smaller tetrasporangia.

Plants were found on the empty shell of *Ensis directus*, mixed with *Conchocelis rosea* Batters and *Ostreobium Quecketii* Born. and Flah., dredged from 25 feet depth of water between Gay Head, Marthas Vineyard and Cuttyhunk Island, Massachusetts, July 17, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 281: B.*

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**Explanation of plate 10**

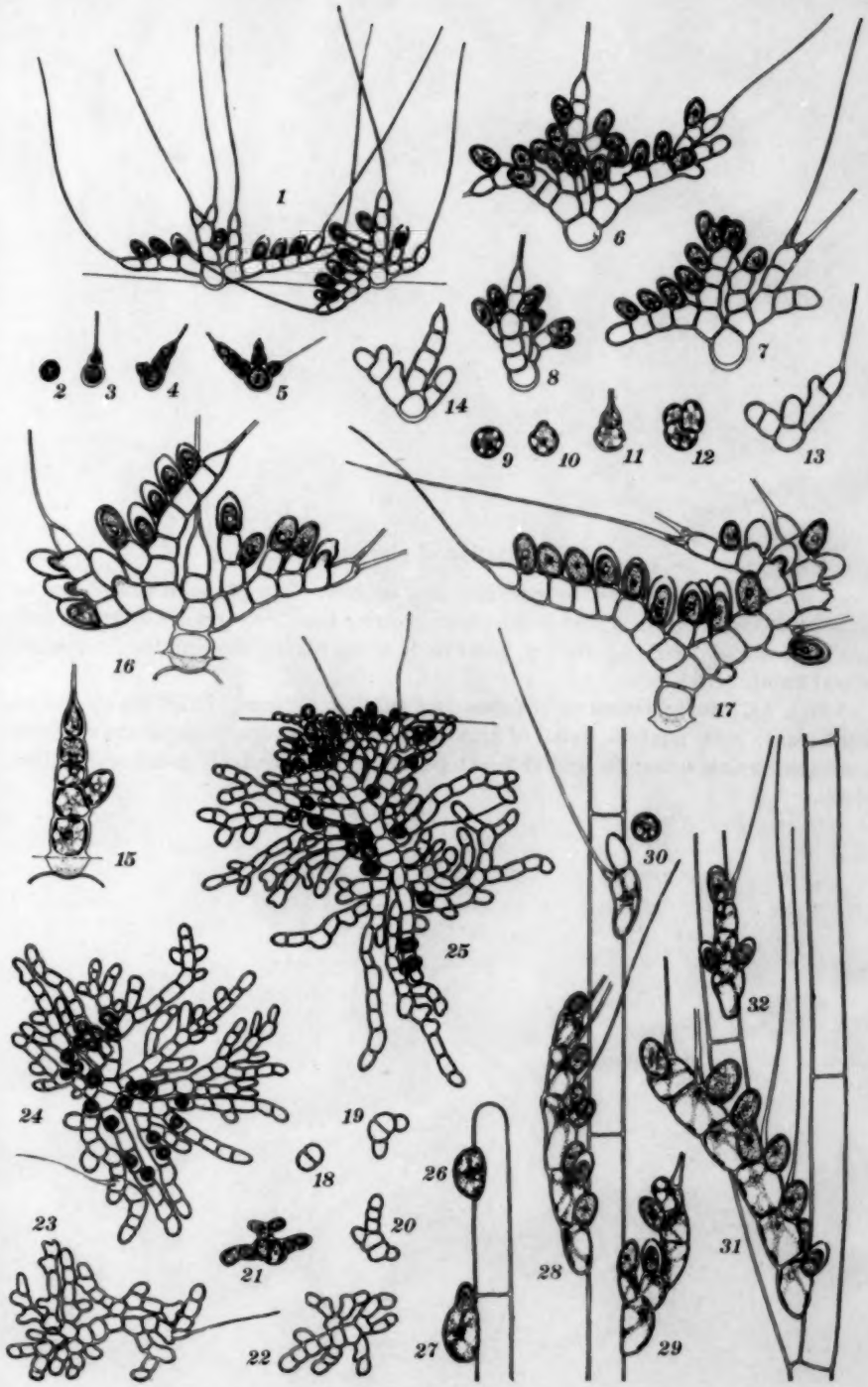
Figs. 1–5. *Acrochaetium microfilum* Jao, sp. nov. ×605. Figure 1, two fully developed plants; figures 2–5, four young plants, showing the earliest developmental stages.

Figs. 6–14. *Acrochaetium compactum* Jao, sp. nov. ×605. Figures 6–8, three well developed plants in different views; figures 9–14, young plants, showing the developmental stages.

Figs. 15–17. *Acrochaetium moniliforme* (Rosenvinge) Børgesen var. *Mesogloiae* Jao, var. nov. ×605. Figure 15, a young plant, showing the earliest ramification, stellate chromatophores, and the much thickened lower wall of the basal cell immersed in the mucilage layer and attached to the peripheral cell of the host; 16 and 17, two adult plants.

Figs. 18–25. *Acrochaetium radiatum* Jao, sp. nov. ×605. Figures 18–23, developmental stage of young plants; figures 24–25, two adult plants.

Figs. 26–32. *Acrochaetium unifilum* Jao, sp. nov. ×605. Figure 26, an undivided germinating spore; figure 27, a germinating spore, showing the earliest stage of the first articulation of the erect filament arising from the upper lateral side of the monospore; figure 30, a dwarf plant composed only of a basal cell, a monosporangium and a hair, the monospore freed from the monosporangium just before drawn; figures 28–29 and 31–32, adult plants in different forms.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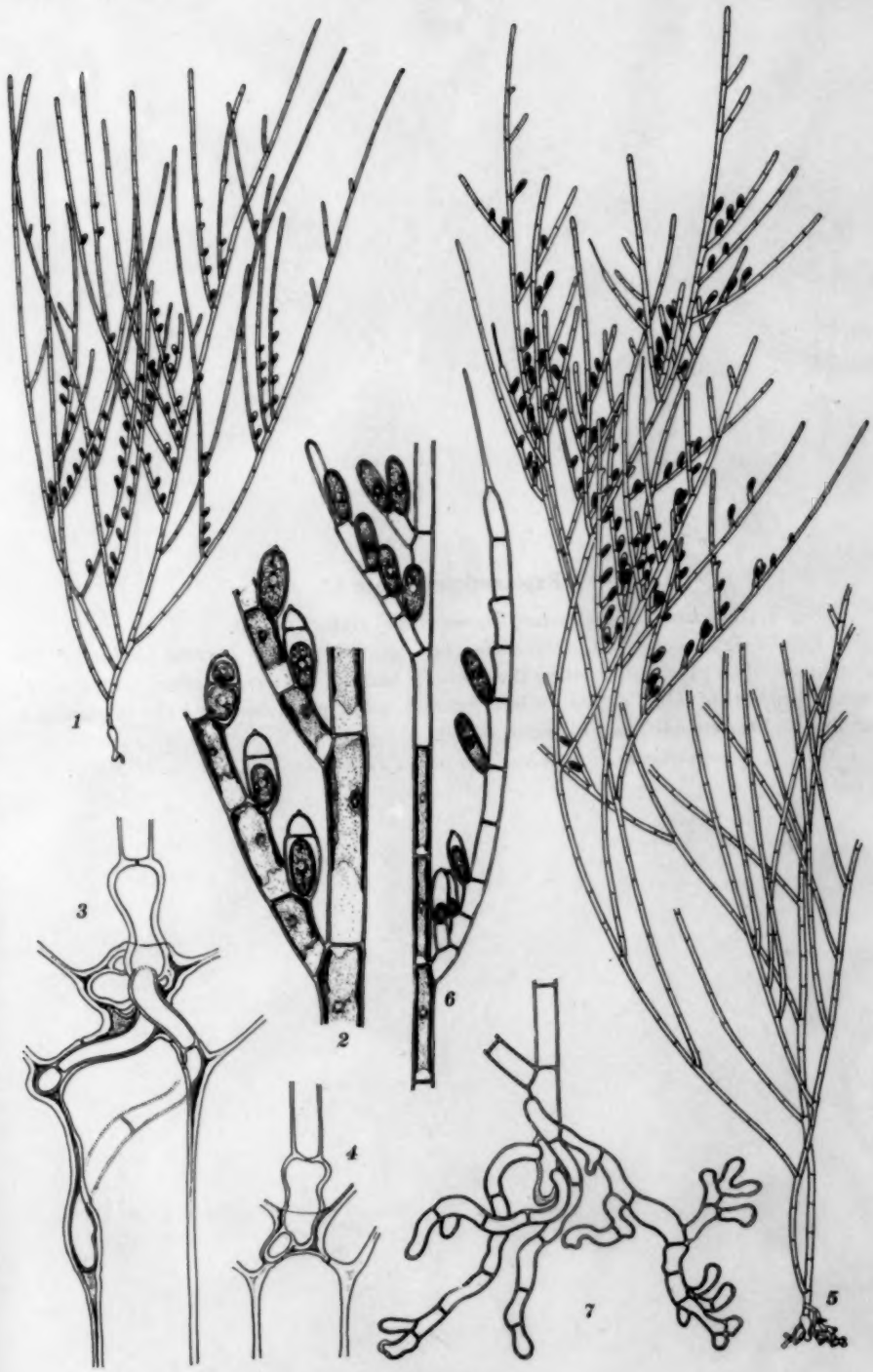
**Explanation of plate 11**

Figs. 1–4. *Acrochaetium intermedium* Jao, sp. nov. Figure 1, habit drawing of an adult plant, ×84; figure 2, part of the plant, showing the structures of vegetative cells and bisporangia, ×605; figures 3–4, basal parts of the plants, showing the intra-membranal habit, ×605.

Figs. 5–7. *Acrochaetium subseriatum* Jao, sp. nov. Figure 5, habit drawing of an adult plant, ×84; figure 6, detail of branchlets bearing monosporangia, showing ripe and regenerating sporangia and chromatophores, ×360; figure 7, detail of holdfast, ×360.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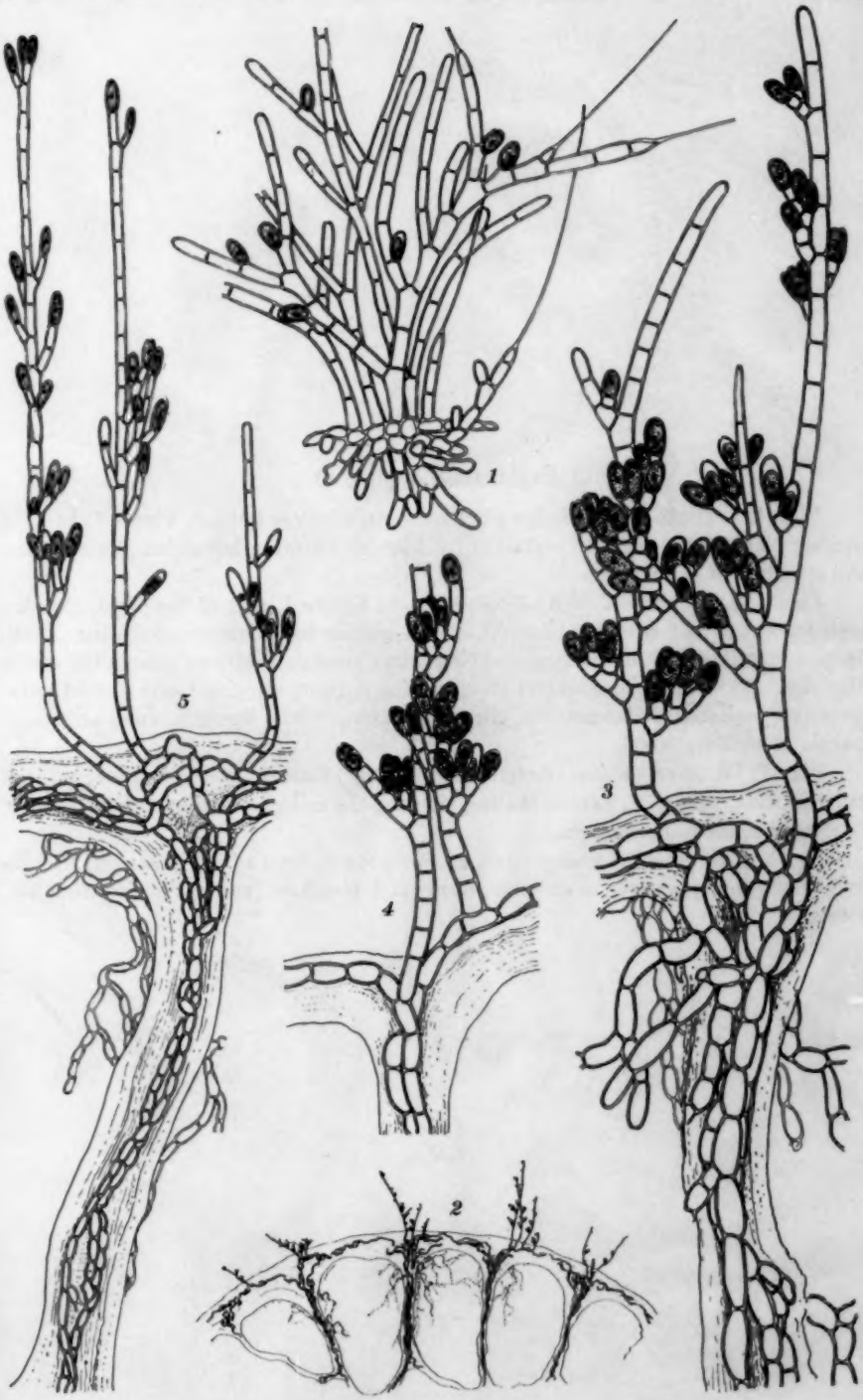
**Explanation of plate 12**

Fig. 1. *Acrochaetium attenuatum* (Rosenvinge) Hamel, ×360.

Figs. 2–4. *Acrochaetium Alcyonidiae* Jao, sp. nov. Figure 2, cross section of *Alcyonidium Mytili* Dalyell, showing the endozoic habit of the *Acrochaetium* plants, ×42, figure 3, detail of adult plants, ×360, figure 4, adult plant, showing the bisporangia and part of the epizoic basal filament, ×360.

Fig. 5. *Acrochaetium Alcyonidiae* Jao var. *cylindricum* Jao. var. nov. ×360.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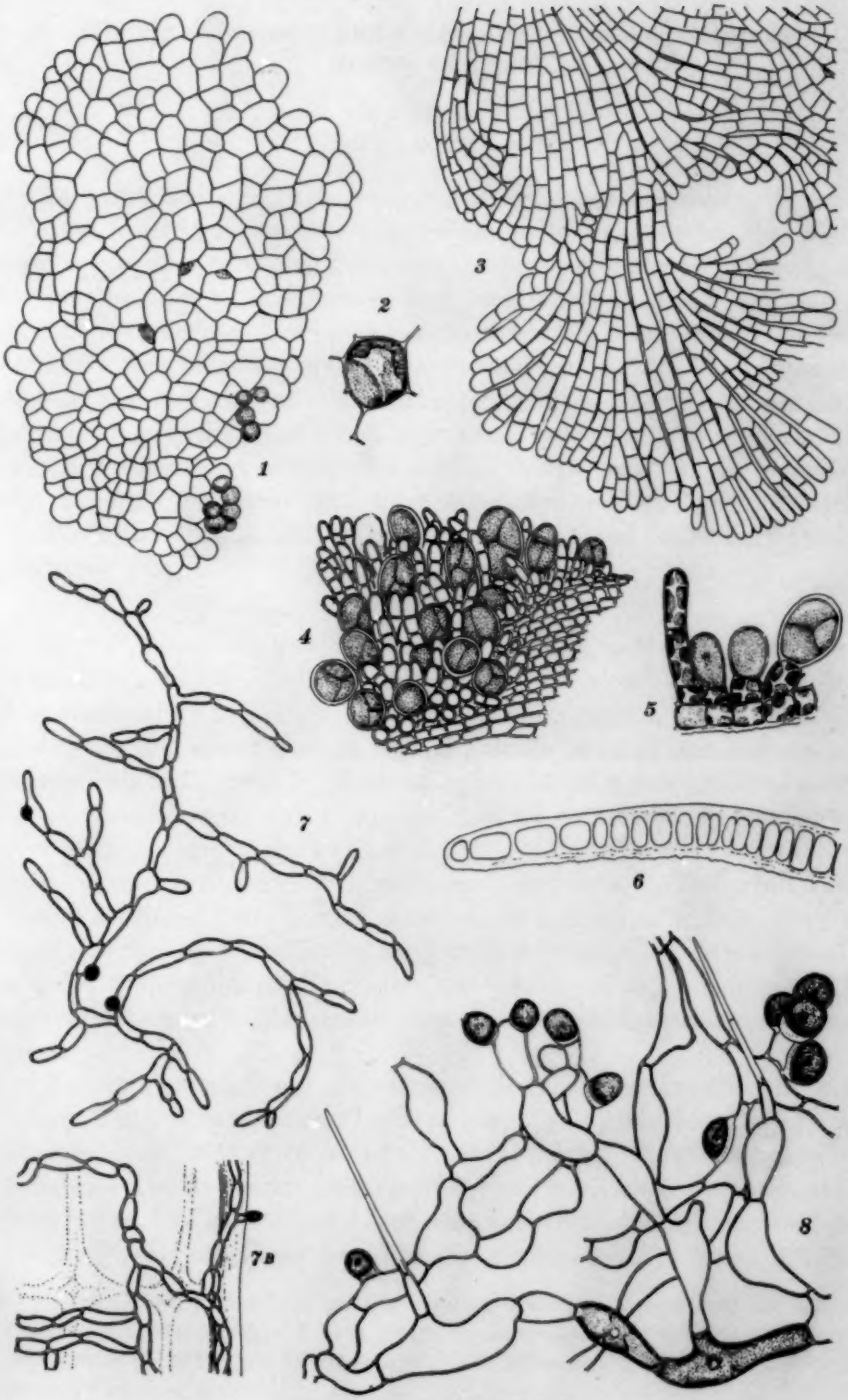
**Explanation of plate 13**

Figs. 1, 2. *Erythropeltis discigera* Schmitz var. *Flustrae* Batters. Figure 1, habit of fruiting plant, ×360, figure 2, detail of fruiting cell, showing formation of monospore and structure of chromatophore, ×750.

Figs. 3–6. *Cruoriopsis Ensisae* Jao, sp. nov. Figure 3, part of the plant, showing arrangement of filaments, ramification, and irregularly lobed margin of thallus, ×360, figure 4, detail of fruiting portion, showing tetrasporangia scattered among the sterile filaments, ×360, figure 5, cross section of fruiting portion, showing 1-cell stalked tetrasporangia and sterile filament and chromatophores, ×605, figure 6, cross section of margin of thallus, ×605.

Figs. 7, 7B. *Acrochaetium emergens* (Rosenvinge) Hamel. ×605. Figure 7, habit of fruiting plant, figure 7B, part of thallus, showing the endophytic filaments and a free, 1-cell stalked monosporangium.

Fig. 8. *Colaconema americana* Jao, sp. nov. ×605. Part of interweaving, fruiting thallus bearing sporangia in different forms and positions, and cylindrical free filaments.




JAO: RHODOPHYCEAE

# A study of blossom bud differentiation in the McIntosh variety of apple[1]

ISADOR AARON

(WITH PLATES 14 AND 15)

The work herein reported was conducted during the growing season in 1931, to investigate the possible correlation between the morphological condition of the primordial meristem and blossom bud development; and the possible correlations between such treatments as nitrate application, girdling and scoring of the trees and blossom bud development. This was done in order to develop an indicator which would enable one to determine much earlier in the season than had been possible before, which buds would become blossom buds and which buds would become vegetative buds. The principal morphological character used for this purpose was the breadth of the primordial meristem. Spur buds alone were studied, since the process of differentiation is similar for both the spur bud and the axillary buds of the apple tree.

## METHODS

In the present study, buds were taken from the McIntosh variety of apple. The trees were budded on ordinary French crab seedlings, used as rootstocks. Only buds from spurs two or more years old were used. The buds were prepared for study by the paraffin method, and stained with Flemming's triple stain. To eliminate xylol and the higher grades of alcohol n-butyl alcohol was used. Continued soaking in paraffin for as long as a year made microtome work easier. A sliding microtome was used, to secure sections around 10$\mu$ thick. The meristem breadths of the buds removed up to and including July 14 were measured in microns. The breadth of the buds removed up to and including July 14 were measured in microns. The breadth of the primordial meristem was considered to be the distance between the bases of the nearest scales occuring on opposite sides of the meristem.

By random selection, the buds were removed from six selected trees at intervals of 4–7 days, on and between May 2 and July 14, on July 29, and September 18, 1931. Two of the trees were girdled, the girdle being 5–10 mm. wide, two of the trees were scored with two sharp knife cuts, and two were uncut. The girdled and scored trees were treated in this way each year for three years preceding the beginning of this study. On March 17, 1931,

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sodium nitrate was applied to one girdled tree, one scored tree and one uncut tree. The girdling and scoring were done June 8, 1931. Buds were opening May 2. By June 24, bud scales were visible to the naked eye, on the terminal buds. Since there were primordia of blossoms in some of the buds removed July 29, and flower clusters in some of the buds removed September 18, these buds were used only for morphological studies.

Selected meristems were used for photomicrographs. A magnification of 150× was used for meristems alone, and one of 73× for other details.

## RESULTS

The percentage of spur blossom buds on each of these trees was determined by actual count, the following spring. This percentage, given in table 1, is the proportion of these spur buds remaining on the tree, after

TABLE 1

*Statement concerning buds removed from and left on tree, and blossom buds on tree at blooming time, 1932*

| TREE | TOTAL NO. OF BUDS ON TREE | NO. OF BUDS LEFT AFTER SAMPLING WAS COMPLETED | % OF BLOSSOM BUDS, FOUND BY ACTUAL COUNT IN SPRING OF 1932 | NUMBER AND PER CENT OF TOTAL BUDS IN SAMPLES AT PERIODS STATED | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | MAY 2 TO JUNE 8 | | JUNE 12 TO JUNE 24 | | JUNE 29 TO JULY 14 | | MAY 2 TO JULY 14 | |
| | | | | NO. | % | NO. | % | NO. | % | NO. | % |
| Ungirdled minus nitrates | 1024 | 793 | 42.0 | 67 | 6.5 | 88 | 8.6 | 76 | 7.4 | 231 | 22.5 |
| Girdled minus nitrates | 1693 | 1497 | 79.3 | 61 | 3.0 | 62 | 3.0 | 73 | 4.3 | 196 | 11.5 |
| Girdled plus nitrates | 1435 | 1223 | 42.8 | 58 | 4.0 | 74 | 5.1 | 80 | 5.6 | 212 | 14.7 |
| Scored minus nitrates | 1044 | 853 | 74.9 | 69 | 6.6 | 59 | 5.7 | 63 | 6.0 | 191 | 18.3 |
| Scored plus nitrates | 1221 | 1008 | 39.7 | 64 | 5.2 | 62 | 5.1 | 87 | 7.2 | 213 | 17.4 |
| Ungirdled plus nitrates | 1613 | 1395 | 66.1 | 68 | 4.2 | 74 | 4.6 | 76 | 4.7 | 218 | 13.5 |

sampling was completed in 1931, that opened in the spring of 1932 to produce bloom. In this table the buds collected at shorter intervals were combined, so that those collected between May 2 and June 8 constitute one sample, those collected from June 12 to June 24 a second sample, and those collected from June 29 to July 14 a third sample. In this table the treatment of the tree, the total number of buds on the tree at the beginning

TABLE 2

*Meristem breadths and blossom production*

| TREE | % BLOSSOM BUDS BY ACTUAL COUNT | BREADTH OF MERISTEMS (MICRONS) | PER CENT OF TOTAL BUDS MEASURED WHICH WERE AT OR ABOVE THE MICRON BREADTH INDICATED | | | |
|---|---|---|---|---|---|---|
| | | | MAY 2–JUNE 8 | JUNE 12–JUNE 24 | JUNE 29–JULY 14 | MAY 2–JULY 14 |
| Ungirdled minus nitrates check | 42.01 | 130 | 62.7 | 73.9 | 89.5 | 75.5 |
| | | 140 | 56.7 | 64.8 | 86.8 | 69.7 |
| | | 150 | 40.3 | 50.0 | 68.4 | 53.2 |
| | | 160 | 35.8 | 45.4 | 60.5 | 47.6 |
| | | 170 | 25.4 | 35.2 | 52.6 | 38.1 |
| | | 180 | 23.9 | 28.4 | 47.3 | 23.3 |
| | | 190 | 16.4 | 19.3 | 35.5 | 23.8 |
| | | 200 | 14.9 | 13.6 | 31.6 | 19.9 |
| Girdled minus nitrates | 79.29 | 130 | 86.8 | 91.9 | 98.6 | 92.9 |
| | | 140 | 81.9 | 87.0 | 98.6 | 89.8 |
| | | 150 | 68.8 | 85.5 | 97.3 | 84.7 |
| | | 160 | 62.3 | 79.0 | 93.2 | 79.1 |
| | | 170 | 54.0 | 66.1 | 84.9 | 69.4 |
| | | 180 | 39.3 | 58.0 | 75.3 | 58.7 |
| | | 190 | 36.0 | 48.4 | 67.1 | 51.5 |
| | | 200 | 32.8 | 33.8 | 53.4 | 40.8 |
| Girdled plus nitrates | 42.76 | 130 | 70.7 | 72.9 | 91.3 | 79.2 |
| | | 140 | 67.2 | 66.2 | 88.8 | 75.0 |
| | | 150 | 48.3 | 48.6 | 70.0 | 56.6 |
| | | 160 | 39.7 | 37.8 | 66.3 | 49.0 |
| | | 170 | 27.6 | 25.7 | 52.5 | 36.3 |
| | | 180 | 20.7 | 24.3 | 46.3 | 31.6 |
| | | 190 | 15.5 | 12.2 | 42.8 | 21.2 |
| | | 200 | 13.8 | 10.8 | 26.3 | 17.5 |
| Scored minus nitrates | 74.91 | 130 | 81.1 | 88.1 | 98.4 | 89.0 |
| | | 140 | 69.6 | 88.1 | 96.5 | 84.3 |
| | | 150 | 65.2 | 76.3 | 88.9 | 76.4 |
| | | 160 | 60.9 | 66.1 | 74.6 | 67.0 |
| | | 170 | 49.3 | 54.2 | 54.0 | 52.4 |
| | | 180 | 39.1 | 47.5 | 44.4 | 43.5 |
| | | 190 | 27.5 | 33.9 | 33.3 | 31.4 |
| | | 200 | 24.6 | 15.2 | 22.2 | 20.9 |
| Scored plus nitrates | 39.68 | 130 | 71.8 | 80.6 | 90.8 | 82.1 |
| | | 140 | 62.5 | 69.3 | 87.3 | 74.6 |
| | | 150 | 45.3 | 46.8 | 66.7 | 54.5 |
| | | 160 | 43.7 | 43.5 | 64.4 | 52.1 |
| | | 170 | 31.2 | 33.9 | 51.7 | 40.4 |
| | | 180 | 28.1 | 30.6 | 47.1 | 36.6 |
| | | 190 | 24.3 | 25.8 | 39.1 | 30.5 |
| | | 200 | 18.7 | 25.8 | 28.7 | 24.9 |

TABLE 2 (*Continued*)

| TREE | % BLOSSOM BUDS BY ACTUAL COUNT | BREADTH OF MERISTEMS (MICRONS) | PER CENT OF TOTAL BUDS MEASURED WHICH WERE AT OR ABOVE THE MICRON BREADTH INDICATED | | | |
|---|---|---|---|---|---|---|
| | | | MAY 2–JUNE 8 | JUNE 12–JUNE 24 | JUNE 29–JULY 14 | MAY 2–JULY 14 |
| Ungirdled plus nitrates | 66.09 | 130 | 75.9 | 94.6 | 92.2 | 88.0 |
| | | 140 | 63.2 | 89.2 | 85.9 | 80.7 |
| | | 150 | 48.5 | 71.6 | 78.9 | 67.0 |
| | | 160 | 45.6 | 67.6 | 73.7 | 62.8 |
| | | 170 | 30.9 | 55.4 | 64.5 | 50.9 |
| | | 180 | 27.9 | 45.9 | 61.8 | 45.9 |
| | | 190 | 25.0 | 31.1 | 55.3 | 37.6 |
| | | 200 | 23.5 | 27.0 | 47.4 | 33.0 |

of the study, the percentage of this total removed for each sample, and the number of buds remaining on each tree are also given.

In table 2 are given the results of the measurements of the meristem breadths. An examination of the data presented in this table indicates a correlation between the breadth of the meristem and the number of blossom buds formed. These meristems increase in breadth as the growing season advances. There is a definite tendency for the correlation between the breadths of the primordial meristems and the percentage of blossom buds to occur at ever greater breadths through the growing season. The increase in breadth of these meristems is a continuous progression from the beginning of the growing season until the appearance of primordia of blossom clusters later in the summer. The primordial meristems that will differentiate into blossom clusters are most likely broad meristems.

Table 3 presents the results of statistical analysis. For each sample and for the total meristems removed from each tree, the mean of the breadth measurements is given. In each case the significance of the mean of each treated tree, as compared with the mean of the uncut tree not treated with nitrates, is given. The uncut tree not treated with nitrates is considered as a check. When compared with the mean of the check, the significance of the mean of the treated tree can be found.

The data of table 3 indicate that, while the mean of the breadths is greater with each successive sample of buds, this increase seems to occur without any relationship to treatment. In regard to significance of such treatments as girdling or the use of nitrates the results seem too variable for an inference to be made.

In the process of study of the morphology of the meristems, a line is drawn to connect the bases of the nearest scales. This line is called a chord. The depth of the meristem is the distance from the crest of the meristem

to the chord. Data on the examples cited are presented in table 4, and consist of measurements of these meristems.

In relation to the morphology of these meristems, the provascular form, the changes in form of the primordial meristem, and the primordia that arise from it in the process of blossom bud differentiation were studied. The provascular form is the ring of procambium strands surrounding the pith at the tip of the fruit spur. While the number of layers of cells in the meristem were too variable to be used as an indicator, changes in the shape of the provascular form and in the form and depth of the meristem were of value in the study of blossom bud differentiation.

TABLE 3

*Significance of the means of meristem breadth measurements of treated trees*

| TREE | MAY 2–JUNE 8 | | | JUNE 12–24 | | | JUNE 29–JULY 14 | | | MAY 2–JULY 14 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BUDS STUDIED | MEAN IN $\mu$ | SIGNIFICANCE | BUDS STUDIED | MEAN IN $\mu$ | SIGNIFICANCE | BUDS STUDIED | MEAN IN $\mu$ | SIGNIFICANCE | BUDS STUDIED | MEAN IN $\mu$ | SIGNIFICANCE |
| Ungirdled minus nitrates check | 67 | 145.4 | — | 88 | 156.8 | — | 76 | 175.5 | — | 231 | 159.7 | — |
| Girdled minus nitrates | 61 | 177.1 | 6.8 | 62 | 186.5 | 7.5 | 72 | 206.9 | 7.6 | 196 | 191.1 | 12.3 |
| Ungirdled plus nitrates | 68 | 159.7 | 3.2 | 74 | 161.4 | 1.3 | 74 | 192.4 | 4.4 | 218 | 175.9 | 6.4 |
| Scored plus nitrates | 64 | 153.6 | 1.8 | 62 | 164.3 | 1.7 | 87 | 176.8 | 0.3 | 213 | 166.8 | 3.0 |
| Scored minus nitrates | 69 | 168.4 | 5.3 | 59 | 174.2 | 4.4 | 63 | 177.1 | 0.4 | 191 | 173.1 | 5.6 |
| Girdled plus nitrates | 58 | 168.3 | 5.2 | 74 | 152.4 | 1.3 | 80 | 173.0 | 0.6 | 212 | 160.0 | 0.1 |

In the process of blossom bud differentiation the shape of the provascular form, and the form of the primordial meristem, constantly change, and the depth of the meristematic mass increases. The author has divided this process of change in dimensions and visible form into arbitrary stages. While a leaf or scale is being produced from the primordial meristem, the outline of the meristem is a flat, more or less broken line. This is stage 1 (pl. 14, fig. 1). After the primordium of the scale or leaf is produced, the flat broken outline of the primordial meristem disappears and changes into the form of the arc of a circle. Cell division seems to fill in the arc. Stage 2 (pl. 14, fig. 3) represents this condition.

In stage 3 (pl. 14, figs. 4, 6; pl. 15, fig. 1) the primordial meristem undergoes a series of changes. Though the arc-like form of the meristem is retained for an interval, the margin of the meristem outline develops a curve of its own, so that the arc-like form seems to rest upon the upper boundary of the margin. Finally, cell division away from the center tends to reduce the curvature of the meristem to such a degree that the meristem resembles

a plateau with long and steep slopes. The arc-like curvature has been constantly disappearing until the plateau has been formed. With more cell division, the flat upper surface of the plateau becomes distorted, and the slopes of the plateau become obscured as the distortion proceeds. The depth of the primordial meristem constantly increases, and the distortion becomes greater, until this meristem is a large distorted mass of tissue (pl. 14, fig. 6; pl. 15, fig. 1).

The provascular form is hemispherical in the first two stages and the early part of stage 3 (pl. 14, fig. 2). As the form of the meristem becomes distorted, the shape of the provascular form becomes more conical. When the primordial meristem has become a distorted mass of tissue the provascular form is broadly conical in shape.

In the production of leaves and scales all primordial meristems pass through the first two stages and the early part of stage 3. The primordial meristem does not assume the form of a plateau. Preceding the appearance of a scale or a leaf, the meristem becomes deeper and more arc-like. Following this appearance, the meristem is shallow, with its surface a more or less flat broken plane. The appearance of each scale and leaf primordium seems to be preceded and followed by this sequence of events. The provascular form is always hemispherical in shape.

Until the primordial meristem enters stage 4 it is a simple mass of tissue. After the meristem enters this stage, primordia of blossoms arise from it. By a process of separation and cell division a succession of primordia forms (pl. 15, figs. 2, 3, 5). For the sake of clarity it can be assumed that the primordial meristem has ceased to exist, being transformed into primordia. There are formed a terminal (central) primordium and lateral primordia. The lateral primordia become leaves or bracts. From the sides of the terminal primordium arise more lateral primordia as the terminal primordium retains its identity, and, by cell division, increases in volume and dimensions. Finally, after a number of leaves or bracts have been produced, the terminal primordium develops into a terminal blossom, while each of the most recently developed lateral primordia develops into a lateral blossom, each lateral blossom being in the axil of a bract.

From the first alteration of the deep, broad and distorted primordial meristem into the terminal primordium and the first lateral primordia, until the most recent primordia become blossoms, the sequence of the appearance of the primordia is a matter of repetition. Until the terminal primordium becomes a blossom, there is always a terminal primordium 80–150$\mu$ broad to continue the process of generation. The appearance of the blossoms represents the completion of a developmental progression.

With this process of change from the distorted primordial meristem

into a blossom cluster, the provascular form has changed from a shape broadly conical to one that is a long attenuated cone.

In table 4 measurements of the examples cited are given. They merely illustrate the point that a primordial meristem increases in breadth and

TABLE 4

*Dimensions of meristems and primordia*

| PLATE | FIGURE | MICRONS BREADTH OF PRIMORDIAL MERISTEM | MICRONS BREADTH OF TERMINAL PRIMORDIUM | DEPTH MICRONS | STAGE |
|---|---|---|---|---|---|
| 14 | 1 | 136 | | 13 | 1 |
| 14 | 3 | 260 | | 42 | 2 |
| 14 | 4 | 240 | | 64 | 3 |
| 14 | 6 | 240 | | 123 | 3 |
| 15 | 1 | 265 | | 147 | 3 |
| 15 | 2 | 247 | 150 | 167 | 4 |
| 15 | 3 | | 80 | 143 | 4 |
| 15 | 5 | | 150 | | 4 |

depth while differentiating into a blossom cluster. No primordial meristems less than 220$\mu$ broad were observed to differentiate into blossom clusters.

## DISCUSSION

Stating briefly the development of the flower cluster of the apple, Kraus (1913) writes that "the first observable indication of the flower is the more or less thickening of the axis. Minute bracts, in the axils of which are found blunt protuberances, arise from it in a very close spiral. The tip of the axis never loses its identity, but on the contrary enlarges considerably and always develops slightly in advance of the protuberances immediately below it. Later these protuberances develop into definite individual flowers."

Many workers, including Drinkard (1909–10), have attempted to recognize the early stages of blossom bud formation. It has been observed that first the growing point flattens, and then it thickens and rises above the bases of the nearest scales as the flower cluster is about to appear. Many disagree about the breadth of the primordial meristem as a criterion in the recognition of the early stages of blossom bud differentiation. The corrugation of the primordial meristem is considered by Drinkard as the earliest indication of blossom bud differentiation. Neither the breadth nor the rising of the meristem above the bases of the nearest scales before it becomes corrugated seem to be considered as matters of importance.

Much work has been done on the differentiation of flowers from meristems. This report deals with the diameter of the primordial meristem in

relation to the differentiation of the blossom bud of the McIntosh variety of apple. On the basis of the work done in this study, the following inferences seem justified by the results obtained. There is correlation between meristem breadth and blossom formation. The breadths increase from the time of bud break in the spring until flower buds begin to form and vegetative buds become dormant. Flower buds probably develop from broad meristems.

Breadth is a relative term. A primordial meristem considered broad on May 8 may not be considered broad on July 7. Breadth is related to time, and should be considered in terms of range rather than precise size. Primordial meristems that differentiate into blossom buds are probably even broader than the data of table 2 would indicate. For blossom clusters to differentiate, the primordial meristems must be of a breadth of at least 220$\mu$.

There is a tendency for the mean of the breadths of the primordial meristems to increase in succeeding sampling periods. There was too much variation in the statistical data for a statement on the effects of the treatments to be made. The results of statistical analysis do not deny that treatment may influence fruit bud formation. They merely indicate the danger of relying on too few trees for evidence. The results of culture, as girdling or nitrate application, can be governed by the number of individuals treated. In several cases the author observed variations in the number of flower clusters on different limbs of the same tree, even on some girdled trees. With a small number of trees, injury and biennial bearing might influence results when differences in culture are compared.

A division of blossom bud formation into a series of stages is possible. Though arbitrary, these stages illustrate a continuous process of development. All primordial meristems pass through stages 1 and 2, and through the early part of stage 3. The differences consist of events that happen afterward.

Concerning the breadth of the primordial meristem from which a blossom cluster will be differentiated, opinion is divided. Black (1916), Kirby (1918), and Goff (1899) state that the development occurs when a broad meristem is present. They believe that in the vegetative bud the growing point is narrow (Goff, 1899); that the inflorescence will develop from a broad growing region (Black, 1916); that when flower bud differentiation is occurring, the meristem thickens, its crest rises above the bases of the nearest scales, and its outline becomes irregular (Goff, 1899). Kirby (1918) reported that, in the apple varieties he studied, the crown of a leaf bud was found to be less than 0.14 mm. while the crown of a flower bud was 0.27 mm. broad during the period of flower bud differentiation.

Many workers believe that a broad primordial meristem is not a reliable indicator of blossom bud differentiation (Bradford, 1915; Magness, 1916; Rasmussen, 1930). They place more reliance on a narrow meristem as an indicator of this differentiation. In the consideration of such a matter as broad and narrow, the determination must first be made of what dimension is broad and what dimension is narrow.

Believing that there has been confusion regarding the "first stage of fruit bud formation," Bradford (1915) considers the matter in detail. He states that the undifferentiated crown "must be regarded as potentially either a leaf bud or a fruit bud." Though some have considered this "as the first stage in fruit bud formation," this structure is found at the tips of one-year-old twigs, and at times in early September. "Long before this time most buds have become differentiated into either leaf buds or fruit buds." He considers the differences between the buds. "Distinct leaf buds, well differentiated, were found as early as May. The leaf buds differ from the undifferentiated in that the crown is broader and flatter, is not raised so high above the level of the embryo leaves and scale bases, and has no swellings or very young leaves at its periphery. The amount of meristematic tissue is relatively less, and clearly defined tissue occurs closer to the growing point. All in all, the appearance presented strongly suggests a resting stage. Whether buds can advance from this resting stage again and form fruit buds in the same season is a matter for conjecture."

In contrast to Bradford the author believes that the so-called resting stage can occur at any time of the year. This is in stage 2. In this stage the meristem outline is like the arc of a circle. The flatness Bradford mentions seems to be the lack of a broken outline.

Such traits do not seem to be restricted to dormant buds. Other buds not in the dormant condition may have them. They may be present at any time, in an undifferentiated bud, a leaf bud producing leaves, a blossom bud in its earliest stages, or in a vegetative dormant bud.

This stage might be called a quiescent stage, to indicate that, at the moment, there is delayed morphological activity between the appearance of two successive primordia from a primordial meristem. The quiescent stage can be a matter of a day or of months. Furthermore, the quiescent stage is not correlated with blossom bud production. Primordial meristems of any breadth can be in this stage. In relation to this, the author believes that leaf buds can be differentiated at any time in the growing season.

There does seem to be some correlation between meristem depth and blossom bud development. Bradford is probably correct in believing that the meristems of undifferentiated and leaf buds seem to have less tissue, with undifferentiated tissue occurring closer to the growing point, and are

less raised above the nearest scale and leaf bases. Meristem depth as the chief criterion, however, can be misleading, for the breadth must be considered merely in relation to very broad meristems at the time visible differentiation of a blossom cluster is occurring.

Bradford also believes that the "first evidence of fruit bud formation" is "the rapid elevation of the crown into a narrow conical form, rounded at the apex, with fibrovascular connections and pith areas advancing concurrently." The succession of changes is rapid. In making this statement, Bradford may not have considered what seems to be the following sequence of events. After the primordium of a bract has formed, the broad primordial meristem has become a narrower terminal primordium. In the succession of lateral primordia following one another from a terminal primordium, with the terminal primordium finally becoming a terminal blossom, the terminal meristematic mass losses breadth and volume. While the breadth and volume of the terminal primordium will increase between the appearance of each preceding and following lateral primordium, events are too rapid for the former dimensions to be regained.

In the production of the lateral primordia of a blossom cluster, something more than cell division occurs. On the lateral portion of the terminal primordium an axis of cell division forms in a definite direction. By a partial separation, due to a kind of dichotomy, some of the lateral portion of the terminal primordium becomes a part of the lateral primordium. In leaf and undifferentiated buds the primordial meristems are not so raised and distorted that the formation of a lateral primordium near the margin is prevented.

The emphasis of Bradford seems to have been placed on the narrowed primordium rather than on the original primordial meristem. Though both resemble a truncated cone, the narrowed primordium is 80 to 150$\mu$ broad, while the less raised primordial meristem is at least 220$\mu$ broad, and is truncated nearer to the base.

Another factor might influence the difference of opinion. As distortion of the meristem occurs, the lower part of the margin differentiates into permanent tissue. Since the greatest breadth is between the bases of the nearest scales, emphasis might be placed on a narrow primordial meristem if the upper part only is considered.

The narrow portion is often broader than the meristems of leaf and undifferentiated buds. The data indicate that the blossom clusters will arise from meristems above a certain breadth range. Given a meristem at or near the lower limit of that range, and given the appearance of permanent tissue in the lower margin of the raised meristem, the illusion of narrowness can be held.

In his consideration of the process of blossom bud differentiation in the axillary buds of the apple, Magness (1916) writes "though a distinct raising and rounding of the crown was apparent" this was not fruit bud differentiation, for by July 9 "many buds had reached this degree of development without forming flower parts." Of the buds collected December 8, the crowns "were well differentiated and rounded evenly," with some "so well developed that had this condition been found earlier in the season they would almost certainly have been mistaken for blossom buds." Before this occurred, the recognition of the blossom bud was impossible. In reporting that the distinctly raised and rounded meristems were poor indicators of blossom bud differentiation, Magness ignored the possibility that competition between primordial meristems might occur. Some buds might be favorably located in regard to external factors. Others might be in a better position to receive the necessary substances. Since blossom bud formation is an exhausting process for the tree, there may not be enough material for primordial meristems that could produce flowers, to do so. Some might be prevented from becoming fruitful. The stage in which this prevention could occur might vary.

Once the process of blossom bud formation begins, it proceeds very rapidly. On any one tree (Kirby, 1918), most of the spur blossom buds form within a month of the time the first blossom buds form. Within the author's collections only the earliest visible stages are seen in the samples of July 14, while most of the stages up to a partial development of the terminal blossom are seen in those of July 29. Rapid differentiation and competitive action among the primordial meristems might account for the broad and merely arc-like meristems, and for those later stages seen by Magness. Furthermore, those who favor the narrow meristem as an indicator must account for the fact that meristems much less than 150$\mu$ broad can be found December 8.

Rasmussen (1930) does not believe that "the broadening of the floral axis, and the development of protuberances described by other investigators" can be considered blossom bud differentiation. He believes that Kirby's idea on the first indication of this differentiation was not clearly stated, and that Kirby (1918) may have confused leaf primordia with the earliest stages of flower bud differentiation. In his consideration of Kirby's work, it should be remembered that an apple flower bud is a mixed bud, with each lateral blossom produced in the axil of a bract. The leaves and bracts of the cluster are produced before the blossoms. The cluster arises from a greatly distorted meristem of at least 220$\mu$ broad. Kirby's presentation is not wrong.

The provascular form seems to be related to the kind of bud produced.

In leaf and undifferentiated buds it is more or less hemispherical, broken at the pole, where cells are not fully differentiated into permanent tissue. This form is retained in stages 1 and 2, and in the early part of stage 3. From then on, the provascular form changes progressively to and through the broadly conical shape, becoming ever more narrowly conical until a very long attenuated cone is present in the fully formed blossom bud. Though the provascular form may vary in each case, there is a definite tendency for it to become ever more conical. The reasons for this change in shape can merely be inferred. While the provascular form is hemispherical, the cells below the meristem seem to be enlarging at the same rate in all directions. After entering well into stage 3, the cell enlargement and cell addition seem to be more rapid in the direction of the longitudinal axis of the spur.

Since the differentiation of the primordial meristem seems to pass through the stages considered, and since this differentiation seems to occur only in the case of meristems at least 220$\mu$ broad, the broad primordial meristem can be considered as an indicator of later blossom bud differentiation. With this statement in mind, a person should be able to make an estimate, at any time in the growing season, of the proportion of blossom buds that will form.

The fate of a primordial meristem may be determined very early in the growing season. Differentiation into a blossom bud is probably determined long before the actual visible appearance of primordia of blossoms occurs. The causes of blossom bud differentiation must be determined. Both meristem breadth and blossom bud differentiation may be results of reactions preceding these events. Such matters as the type and time of treatment of the tree, and previous treatment of the tree, can probably influence the condition of the tree, and can probably aid or retard the conditions that are expressed in fruit bud differentiation.

Certain factors might intercede to alter the fate of a primordial meristem. Of many broad meristems competing for the necessary substances, some will lose out. Though treatment of the tree might alter the intensity of the competition, it would not prevent it; for on girdled trees vegetative spur buds occur, while on uncut nitrated trees broad meristems and blossom clusters appear.

There are many reports dealing with the time of blossom bud differentiation. The time range for trees like the apple has previously been considered to be between the last part of June and the last part of July. On the apple tree differentiation is said to occur earlier in spur than in axillary buds (Gibbs and Swarbrick, 1930; Magness, 1916). In an individual tree the period of differentiation may last a month (Kirby, 1918). In the pres-

ent trend of opinion, the dates of the visible differentiation of the blossom buds will be influenced by the variety, and by ecological factors including culture. The author agrees with Kirby[2] in the belief that the period of time within which most of the blossom buds form is more important than the earliest dates when differentiation into blossom buds occurs in the first buds to become blossom buds.

## CONCLUSIONS

1. The breadth of the primordial meristem of apple buds, as indicated in this study, increases as the growing season advances.

2. There is a definite correlation between time and both the breadth of the primordial meristem and the differentiation of this meristem into a blossom bud.

3. The stages in the differentiation are passed through only after the primordial meristem has become very broad.

4. Rather than one resting stage in the bud of the apple tree, the present study indicates that there is a succession of quiescent stages, in which there is a decreased rapidity of morphological change. The quiescent stages can exist for different periods of time.

5. While the shape of the provascular form seems to be correlated with blossom bud differentiation, it is not as definite an indicator as meristem breadth.

6. One should be able to make a rough prediction, at any time in the growing season, as to the proportion of blossom clusters that will be formed.

7. Concerning the effects of the treatments of the individual, the results as expressed in blossom bud differentiation, were too variable for any inferences to be made.

## ACKNOWLEDGMENT

The author is very grateful to the Department of Horticulture for financing this investigation, to Professor F. N. Fagan, of the Department of Horticulture, for his efforts in initiating the investigation, and for his continuous aid and interest; and to Dr. F. D. Kern and the other members of the botany department for the use of the laboratories in the course of this investigation. Without the valuable advice and constant helpfulness of Professors H. W. Popp, and H. W. Thurston, Jr., of the botany department, the progress of this investigation would have been impossible.

[2] A personal communication, August, 1934.

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## Explanation of plates

High power photomicrographs are magnified 150×, while low power photomicrographs are magnified 72×. Dimensions are given in table 4.

### Plate 14

Fig. 1. This is stage 1. A narrow undifferentiated primordial meristem in a condition of great activity. A primordium of a scale is being produced. The meristem outline is a more or less flat unbroken line.

Fig. 2. Same bud. The provascular form is hemispherical.

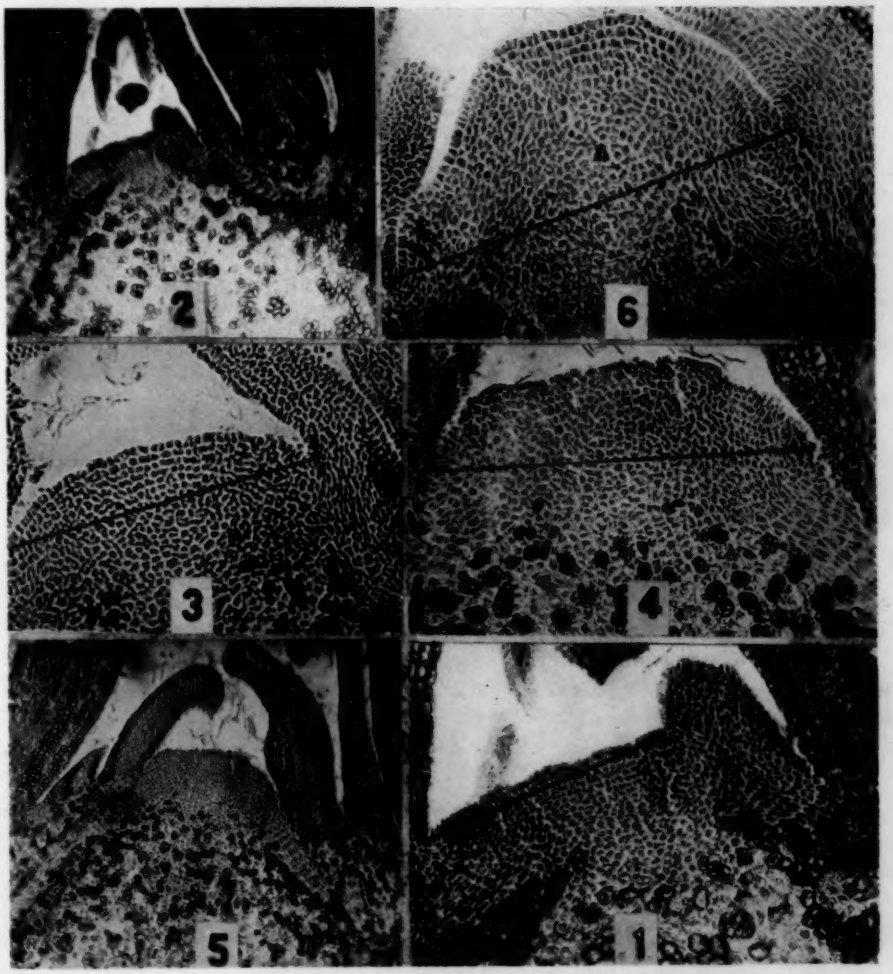
Fig. 3. This is stage 2. The primordial meristem is assuming the curve of an arc of a circle. The margin of the arc touches the bases of the nearest scales.

The following figures of plate 14, and plate 15, fig. 1 are in stage 3.

Fig. 4. The primordial meristem has lost its arc-like curve, and has assumed the form of a highly arched plateau. The meristem is becoming distorted.

Fig. 5. Same bud. The provascular form has become slightly conical.

Fig. 6. Same as plate 15, fig. 1.




AARON: BUD DIFFERENTIATION

## Plate 15

Fig. 1. The primordial meristem is a greatly raised and distorted mass of tissue.

The remaining figures of plate 15 illustrate stage 4. In this stage the primordial meristem has broken into individual primordia.

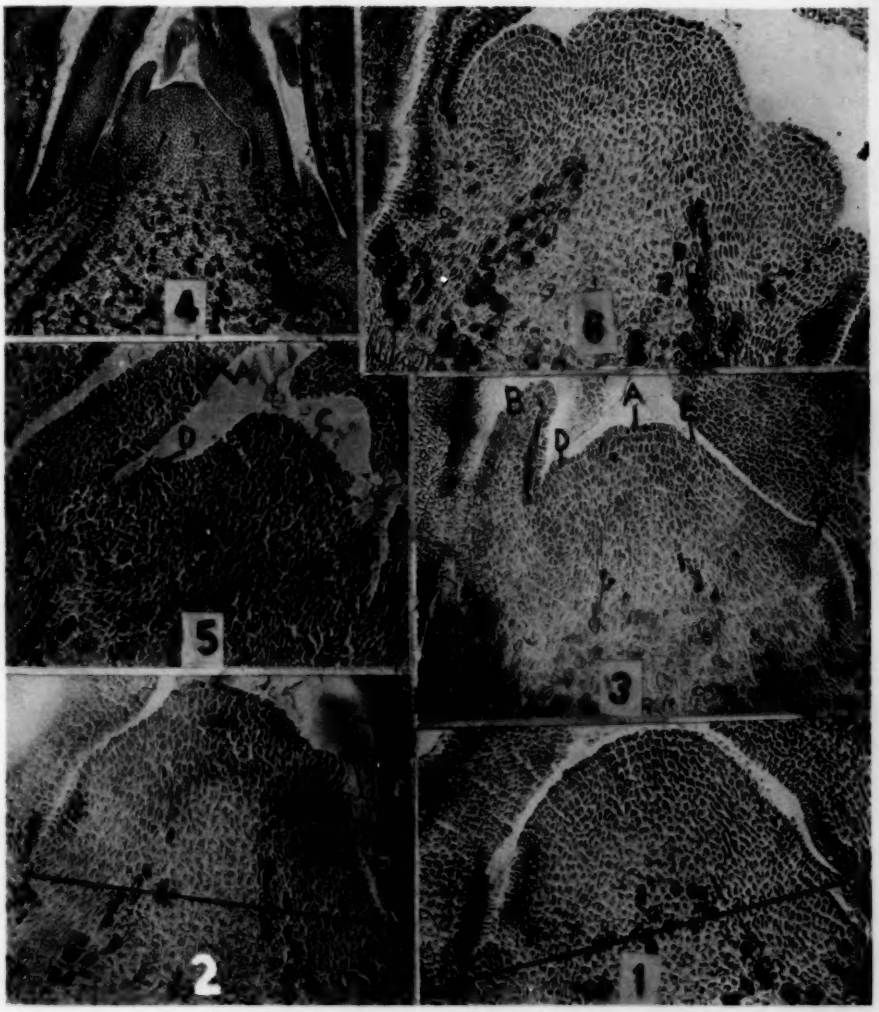
Fig. 2. A terminal (central) primordium and the beginnings of two lateral primordia of leaves or bracts.

Fig. 3. There are present a terminal primordium (A), the well developed primordium of a leaf or bract (B), the base of another well developed leaf or bract primordium (C), and two lateral primordia (D & E) of two more leaves or bracts just beginning to appear.

Fig. 4. The same bud showing a broadly conical provascular form.

Fig. 5. There are present two well developed primordia of bracts or leaves (A & B), a terminal (central) primordium (C), and two lateral primordia (D & E) of leaves or bracts just beginning to appear.

Fig. 6. There are present the primordium of a terminal blossom (the terminal primordium), and the two lateral primordia of two lateral blossoms. In each case the lateral primordium is in the axil of a bract.


4
6
5
3
2
1

# Anatomy of the spikelets and flowers of Carex, Kobresia and Uncinia

ROBERT S. SNELL

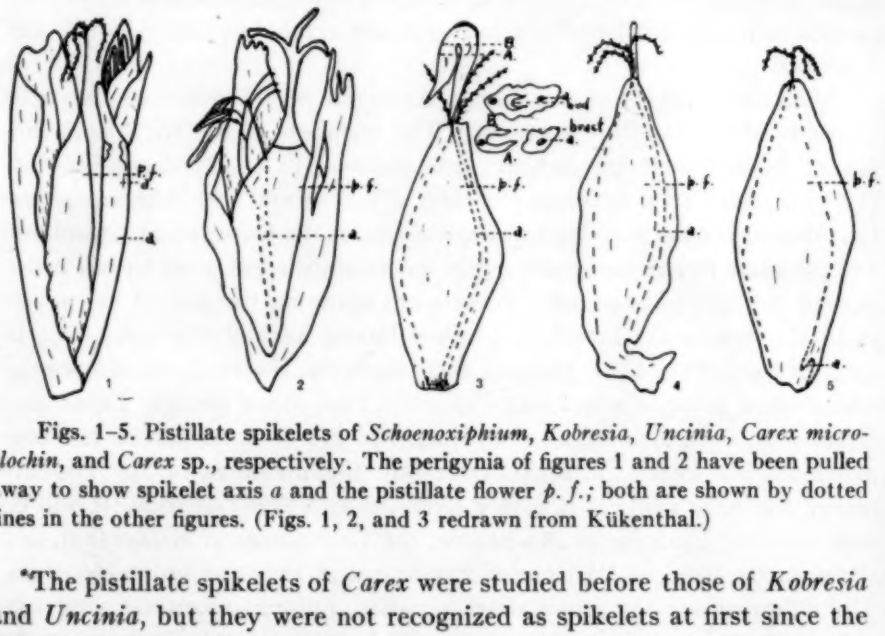
(WITH THIRTY TEXT-FIGURES)

Few problems have received more attention in the literature of plant morphology than has the attempted explanation of the pistillate "flower" of the sedge genus *Carex*. Most of the interest has centered about an interpretation of the morphology of the sac-like structure which immediately surrounds the pistil. (This structure is called the perigynium in American floras.) The status of the present knowledge of the pistillate "flower," with its perigynium, is given in the following pages, and the need for a thorough anatomical study of the "flower" is shown. Later pages give the result of such an anatomical investigation which has been carried on by the author for *Carex* and closely related genera, *Kobresia* and *Uncinia*.

Mackenzie (1931) places *Carex*, *Kobresia*, and *Uncinia* in the tribe Cariceae of the family Cyperaceae. The members of the tribe have unisexual flowers, and the achenes are enclosed in perigynia. Kükenthal (1909) placed *Carex*, *Kobresia* ("*Cobresia*"), *Uncinia*, and *Schoenoxiphium* (an African genus) in the group Caricoideae of the Cyperaceae. Staminate and pistillate flowers are produced in spikes of different order by the members of the group. Staminate flowers are borne on the axis of the spike; pistillate flowers are attached to short lateral axes of the spike, i.e., to spikelet axes. Pax (1889) placed *Carex*, *Kobresia*, *Uncinia*, and *Schoenoxiphium* in a group Caricoideae-Cariceae. Two other genera, *Elyna* and *Hemicarex*, were also included by Pax. Neither of these genera is recognized by Mackenzie or Kükenthal, but the members of the two are placed by these workers in either *Kobresia* or *Schoenoxiphium*. It will be seen that the Cariceae of Mackenzie, the Caricoideae of Kükenthal, and the prior Caricoideae-Cariceae of Pax represent the same group of sedges. The following are the group characteristics: unisexual flowers; a sac-like organ about the pistillate flower; staminate and pistillate flowers, for the most part, borne on axes of a different order.

The genera of the Cariceae, although they have the above characteristics in common, are distinct in many features, especially in the structure of the pistillate spikelet. In *Schoenoxiphium* (fig. 1) the axis of the pistillate spikelet is relatively large and well developed. At its base it bears a single pistillate flower, and usually, toward its tip, several staminate flowers. The pistillate flower, as in all members of the Cariceae, is a simple pistil. The pistil and the base of the axis are nearly enclosed by the perigynium

which in some species is open part way down the posterior side. In *Kobresia* (fig. 2) pistillate spikelets are similar to those of *Schoenoxiphium*, but the axis is not as conspicuous. In some species the axis of the spikelet bears no staminate flowers; in others staminate flowers are usually present. The perigynium is open or partly so, on the posterior side. In *Uncinia* (fig. 3) the axis of the pistillate spikelet is conspicuously exserted from the perigynium, and hooked at the end. The perigynium is completely closed. The axis of the pistillate spikelet of *Carex microglochin* (fig. 4) extends for some distance out of the orifice in the top of the perigynium. In several species of *Carex* (to be described later) the axis approaches the perigynium in length, but is entirely included. In most species the spikelet axis is abortive beyond the attachment of the pistil (fig. 5). In all species of *Carex* the perigynium is closed.




Figs. 1–5. Pistillate spikelets of *Schoenoxiphium*, *Kobresia*, *Uncinia*, *Carex microglochin*, and *Carex* sp., respectively. The perigynia of figures 1 and 2 have been pulled away to show spikelet axis *a* and the pistillate flower *p. f.*; both are shown by dotted lines in the other figures. (Figs. 1, 2, and 3 redrawn from Kükenthal.)

The pistillate spikelets of *Carex* were studied before those of *Kobresia* and *Uncinia*, but they were not recognized as spikelets at first since the spikelet structure is not evident in most of the species of the genus. In fact the interest early manifested in *Carex* centered about the perigynium. This structure is an unusual plant organ which does not lend itself readily to morphological interpretation. What fundamental organ or combination of organs does the perigynium represent?

In 1835 appeared Kunth's explanation of the perigynium and pistillate spikelet of *Carex* which, in the main, is accepted at the present time. Kunth was led to his explanation by a study of a species of *Schoenoxiphium*. According to Kunth the pistillate flower is reduced to a naked pistil borne

on the lateral axis of the spike. It arises in the axil of a large bract which is placed with its back to the main axis. This bract is bicarinate as a result of its position; it surrounds the pistil and lateral axis, and, by the fusion of its margins produces a sac-like covering. Kunth compares the perigynium with the upper palet of grasses, and the subtending bract of the pistillate spikelet of *Carex* with the lower palet of grasses. The perigynium of *Carex* and the upper palet of grasses are the first bracts of small lateral axes, and are called prophylls. The prophylls of a dicotyledonous plant are usually paired, opposite, and lateral. The single prophyll of a monocotyledonous plant lies between the lateral branch and the main axis with its back to the latter. Some dicotyledonous plants seem to have a single prophyll, and some monocotyledons seem to have paired prophylls like those normally found in dicotyledons (Arber, 1925). When there is a single prophyll, it is normally two keeled as a result of pressure against the axis; often there is a vascular strand in each keel. Gay (1838) first compared the perigynium of *Carex* with the prophylls which are found at the bases of the peduncles in many species of the genus; Roeper (1843) elaborated on the work of Gay. The theory that the perigynium represents a single bract with its back to the main axis (a prophyll), a theory founded on the views of Kunth, Gay, and Roeper, did not prevail at this early period, though at a later date it became the established theory.

In 1835 Nees ab Esenbeck regarded the perigynium as composed of two fused bracts, though it is not wholly clear from his geometrical representations what sort of bracts he had in mind. Lindley (1853), whose name became associated with the two-bract theory of the perigynium, groups *Carex*, *Uncinia*, and *Diplacrum* as genera of the Cyperaceae in which two opposite bracts are present. It is evident that Lindley compared the perigynium with non-homologous structures in *Diplacrum*. Robert Brown (1866) held with Lindley that the perigynium represents fused bracts. As with Lindley, Brown homologizes the perigynium with non-homologous structures in other genera (*Iris* and *Diplacrum*).

Payer (1857) introduced the ontogenetic attack on the problem of the perigynium. He concluded from a bud study of the developing perigynium that it is composed of two fused bracts. This conclusion was derived from the fact that the perigynium first appears in the bud as two opposite ridges, one on the right and the other on the left of the subtending bract. These ridges are joined as growth continues in a complete circumference, forming a sac-like perigynium.

It is interesting and significant that Payer worked with a species of *Carex* which possesses a strongly bidentate perigynium. In the ontogenetic development, two ridges appeared first as would be expected in a structure

which at maturity is strongly bidentate at the top. The top of the perigynium appears first, of course, in ontogeny. The teeth at the tip of a mature perigynium are represented at an early stage by two ridges. The rest of the perigynium, the sac-like portion below the teeth, is formed by growth in a continuous ring. In the light of the present knowledge of ontogenetic development generally, how can occurrences in this particular case be interpreted as indicating that the perigynium represents two fused bracts? Both Caruel (1867) and Schumann (1890) have shown that in another species of *Carex* the perigynium starts development as a ring of tissue.

The fact that many species of *Carex* possess rigidly bidentate perigynia and that the perigynia of many species are two-keeled with a strong vascular strand in each keel (these two vascular strands representing the entire supply to the perigynium) is seemingly the strongest evidence for the origin of the perigynium by the fusion of two bracts. Efforts of Lindley and Brown to substantiate the view with comparative morphological data and the effort of Payer to do the same with ontogenetic evidence have failed. Moreover, the bidentate condition of the perigynium seems to follow on its bicarinate nature which is, in turn, a result of the position of the perigynium, with its back against the spike axis. The morphological significance of the vascular strand in the keels is taken up on a later page. It can be said here that the general vascular condition in the perigynia of *Carex* and *Kobresia* does not support the theory that the perigynium arose phylogenetically by the fusion of two bracts.

Kunth's view that the perigynium represents a single bract, placed with its back to the main axis, which found backing and amplification in the work of Gay and Roeper who recognized the perigynium as a prophyll, has become the established view. Caruel (1867), Duval-Jouve (1864), Eichler (1875), Kükenthal (1909), Lotsy (1911), Pax (1885), Townsend (1873 and 1885), and others supported and advanced the theory that the perigynium of *Carex* is a prophyll. The theory that the perigynium represents two fused bracts has received slight support in the more recent literature on *Carex*. Some workers who have regarded the perigynium as a single bract have subscribed to the two-bract theory as an alternative explanation.

That the unit of the pistillate spike of *Carex* is not a flower in the true sense of the word but a spikelet was not realized by many of the early investigators. Interesting, at least, and perhaps significant is the fact that most of those who backed the theory that the perigynium represents fused bracts make no mention of the abortive axis of the spikelet, nor do they indicate that the unit structure in the pistillate spike of *Carex* is a spikelet

and not a flower. Payer refers to the pistillate spikelet as a flower. Lindley says "their flowers" when obviously he means the pistillate spikelets of *Carex*. Kunth and proponents of his theory have generally realized that the pistillate flower of *Carex* consists of a naked pistil only, and that it is the subtending bract of the pistillate flower which forms the perigynium. Later workers recognized it as a prophyll. Their evidence for such an interpretation came largely from comparative morphology; the spikelets of *Kobresia*, *Uncinia*, and *Schoenoxiphium* were used in arriving at a satisfactory explanation of the more obscure pistillate spikelet of *Carex*. The presence of a minute remnant of a phylogenetically aborted axis within perigynia of young spikelets of *Carex* confirmed what comparative morphology strongly indicated.

To Kunth belongs the credit of proposing at an early date (1835) an explanation of the perigynium and spikelet of *Carex* that harmonizes with all later found important evidence, and remains today essentially unhallenged.

As stated in the introduction, it was in part for the purpose of ascertaining, by a thorough anatomical analysis, the actual morphology of the pistillate spikelets, of *Carex* especially, and also of *Kobresia* and *Uncinia* that this investigation was started. An attempt has been made also, by a study of the vascular supply, to arrive at the structure of the ovary and ovule of the *Carex* flower.

## METHODS

Spikelets for study were, in all cases where possible, cut singly from the axis of the spike with specially ground fine-tipped scissors. A small portion of the spike axis where the axis of the spikelet joins it was detached with each specimen. In the case of those species of *Carex* having a very dense spike, a portion of this was taken as a specimen, a procedure employed also with staminate spikes.

Butyl alcohol was used in dehydration and the material was imbedded in hard paraffin. Vascular development in the spikelets is practically complete at flowering time. By taking the spikelets at this early stage or soon after, using butyl alcohol as a dehydrating agent, and employing a hard paraffin, sufficiently thin serial sections could be cut with a rotary microtome. It is, however, impossible to cut spikelets in late fruiting stages by this method. Herbarium material was soaked in warm water or weak alkali solutions as a preliminary treatment.

All of the cross and longitudinal sections employed in this investigation were cut serially, as outlined, in a rotary microtome. All figures of such sections have been drawn directly without the use of camera lucida

or projection apparatus; hence figures represent magnifications of various degrees. Specimens of a given species from different parts of a plant, from different plants, from plants in different places, from plants of more than one season were employed to avoid possible individual abnormalities. Three specimens, at least, were consulted in arriving at any general conclusions on a particular species. It will be seen that most of the species of *Carex* employed are from the northeastern part of the United States. Material of morphologically important species, and of other genera not found in this region, was obtained from herbarium specimens.

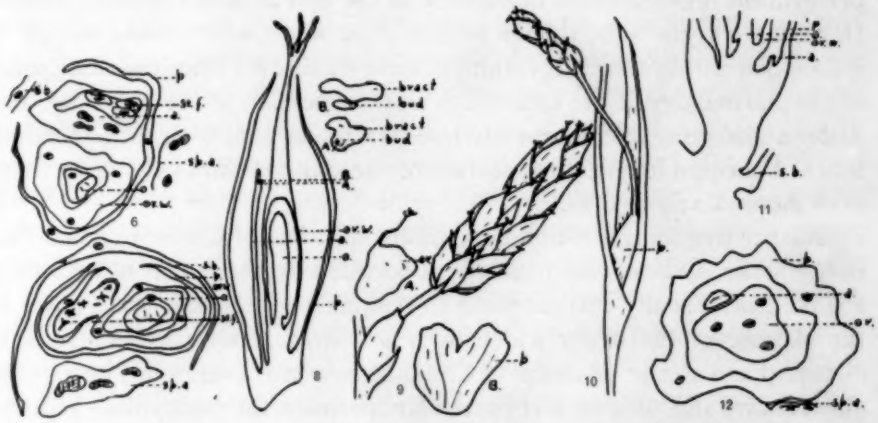
## ANATOMY OF THE PISTILLATE SPIKELETS

Because a detailed knowledge of the pistillate or bisexual spikelets of *Kobresia*, of certain abnormal *Carex* spikelets, and of the pistillate spikelets of *Uncinia* may be of help in understanding the more obscure spikelet condition normally found in *Carex*, these forms are treated first. The bisexual spikelet is found normally in close living relatives of *Carex*, but only in abnormal forms of the genus *Carex* itself. *Kobresia* offers a good example of the probable primitive *Carex* spikelet. The spikelet axis of *Kobresia* does not abort beyond the place of attachment of the pistillate flower, but becomes nearly as long as, or in some cases even longer than the perigynium. In its terminal portion it usually produces one or more staminate flowers with their bracts (figs. 2 and 7). A bisexual spikelet, corresponding to that usually found in *Kobresia* is found abnormally in some species of *Carex*. Normally in *Carex filifolia* the axis of the spikelet is a flat structure of medium length which lies against the achene. But some spikelets of *C. filifolia* which were encountered accidentally, in material which had been taken for sectioning, showed a strictly bisexual state like that in *Kobresia*. In these spikelets the axis is very well developed, and produces two or three staminate flowers near its tip (fig. 6). Within this species such abnormalities are not in any sense common, so far as could be determined, for in the limited amount of material at hand it was impossible by searching to find more of these abnormal spikelets. *Carex eburnea* afforded a less striking abnormality of the type just described in *C. filifolia*. Usually, in this species, it is the axis of the spikelet which is abortive; the ovary, well developed and fertile. In one abnormal spikelet which was sectioned the ovary was abortive; and the axis, a fairly well developed one, produced three abortive stamens. Apparently the axis developed at the expense of the ovary.

There is no fossil evidence to establish a primitive bisexual spikelet in the genus *Carex*. The evidence of comparative morphology favors such a primitive spikelet in *Carex*. Thus the abnormal bisexual spikelets of *C.*

*filifolia* may be reversionary. The abnormality in *C. eburnea* suggests a primitive bisexual spikelet in the genus.

A group of near relatives of *Carex* are set off by themselves, among other things, by a peculiar hook-like spikelet axis (fig. 3). This group is the genus *Uncinia*. Actually, the end of the axis is more than just a hook, as a microscopic examination of serial sections of that region shows. The hooked tip is a bract rolled in from the sides and sharply pointed. A cross section of the axis at the level A (fig. 3A) shows the inrolled bract clearly.




Figs. 6 and 7. Cross sections of an abnormal bisexual spikelet of *Carex filifolia* and a normal bisexual spikelet of *Kobresia caricina*, respectively, to show the similarities.

Fig. 8. Median longitudinal section of the normal pistillate spike of *Carex capitata*. Sections of the spikelet axis at two levels near the tip are shown.

Figs. 9 and 10. Anomalous spikelets of *Carex Schweinitzii* and *C. paupercula*, respectively. The basal prophyll *B* and its contained ovary *A* of *Carex Schweinitzii* are shown.

Figs. 11 and 12. Median longitudinal and cross sections, respectively, of the base of a pistillate spikelet of *Carex Woodii*.

*a*, spikelet axis; *o*, ovule; *ov. w.*, ovary wall; *p.*, perigynium; *s. b.*, subtending bract of spikelet; *sp. a.*, spike axis; *st. f.*, staminate flower.

A similar section at the level B (fig. 3B) shows a bud which the bract subtends. No specimens of *Uncinia* examined (two or three species were available) showed any further development of the bud. However, the report by Bentham (1873) of finding an anther attached to an abnormal seta (axis of the spikelet) of *Uncinia* may mean that the bud which is normally abortive did, in one case, develop (perhaps a reversionary phenomenon) sufficiently to produce at least one stamen. If this surmise is correct, we have another bit of fragile evidence for an ancestral bisexual spikelet for the genus *Uncinia;* hence, evidence for a primitive bisexual spikelet in the closely related genus *Carex*. Certainly there is a prevalence

of bisexual spikelets normal and abnormal, in the genus *Carex* and its near relatives.

Nearly every species of *Carex* shows some remnant of the spikelet axis within the perigynium at flowering time and even later. Usually it is no more than a small knob of tissue with no indication of component organs, such as bracts or a terminal bud (figs. 11 and 12). A few species of *Carex* possess spikelets with long axes, long enough in one case (*C. microglochin*) to extend, along with the stigmas of the pistil, out of the orifice of the perigynium (fig. 4). There is no hook at the end as in the genus *Uncinia*. In *C. capitata* the axis, though shorter than in *C. microglochin* so that it is included within the perigynium, is more significant from the standpoint of the morphology of the spikelet. A close inspection of the top of the axis under a dissecting microscope discloses a terminal bud with its subtending bract. A median longitudinal section of the spikelet shows the same thing even more clearly (fig. 8).

Rather frequently one finds pistillate spikelets of *Carex* in which the, in one sense, spikelet axis develops abnormally to the extent of becoming a spike axis. Usually this excessive development of the axis takes place at the expense of the ovary which does not show at all, or, if present, is distorted and sterile. Material of *C. paupercula* contained a not infrequent abnormality (fig. 10). In this particular specimen the perigynium bore no ovary in its axil. An abnormality of *C. Schweinitzii* is pictured in figure 9. The prophyll at the base of the axis does not look much like a perigynium, but a much distorted ovary was found in its axil. Numerous cases of proliferating spikelets have been reported in the literature of *Carex*: Borner (1913), Duval-Jouve (1864), Hegelmaier (1887), Holm (1896), Reichardt (1861), Ridley (1884), Schulz (1887), Schumann (1890), Thiselton-Dyer (1875), Townsend (1885), Urban (1880), and Wesmael (1863). A good comprehensive account of anomalous spikelets of *Carex* may be had in "Pflanzen-Pathologie und Pflanzen-Teratologie" by Moquin-Tandon (1842).

These anomalous conditions can not hastily be interpreted as reversionary. They occur in species where the axis of the spikelet is normally reduced to a mere vestige. There are proliferations, grotesque aberrations, that can be expected to tell little or nothing about the detailed structure of the primitive spikelets of *Carex*. They do tell, however, that one is dealing with a spikelet in *Carex*, and that the normally abortive axis of the spikelet under certain conditions is capable of prolonged growth. It may possibly be that some of these anomalous cases are not proliferating spikelets at all, but merely normal spikes developing from a basal prophyll. All of the species of *Carex* in which there are separate staminate and pis-

tillate spikes have prophylls at the bases of the peduncles. These normally are not fertile, i.e., they do not bear pistillate flowers in their axils, but they may under abnormal conditions do so. Prophylls at the bases of the lower peduncles of the inflorescence are usually sheath-like and hyaline, entirely covered by the sheaths of the leaves subtending the lateral axes on which the prophylls are borne, but the prophylls of the upper peduncles are often partially exposed to the elements because subtending leaves in this region are short and bract-like with small or no leaf sheaths. In general the upper prophylls are heavier in texture and have more the appearance of perigynia than do the lower. Anomalous growths of the types that have been described may represent proliferated spikelets or they may represent normal spikes that grow from abnormal prophylls. Perhaps such growths are of two distinct kinds. Perhaps, in a general way, those in which the prophyll subtends a pistil represent abnormally developed spikelets, while those in which the prophyll subtends no pistil are true spikes with perigynium-like prophylls. The present knowledge of abnormalities is so meager that there is no basis for a convincing interpretation of them. That these shoots are reversionary, of course, can not be denied as a possibility. From the normal spikelets of *Kobresia* and *Schoenoxiphium*, and from occasional abnormal spikelets of forms like *Carex filifolia*, the evidence is strong that the ancestral spikelet of *Carex* was bisexual, staminate at the apex and pistillate at the base. It is quite possible, too, that reduction, in some cases at least, has occurred from spikelets which were pistillate in their extremities. The same type of spikelet may not be ancestral to the pistillate spikelets of all present day species of *Carex*.

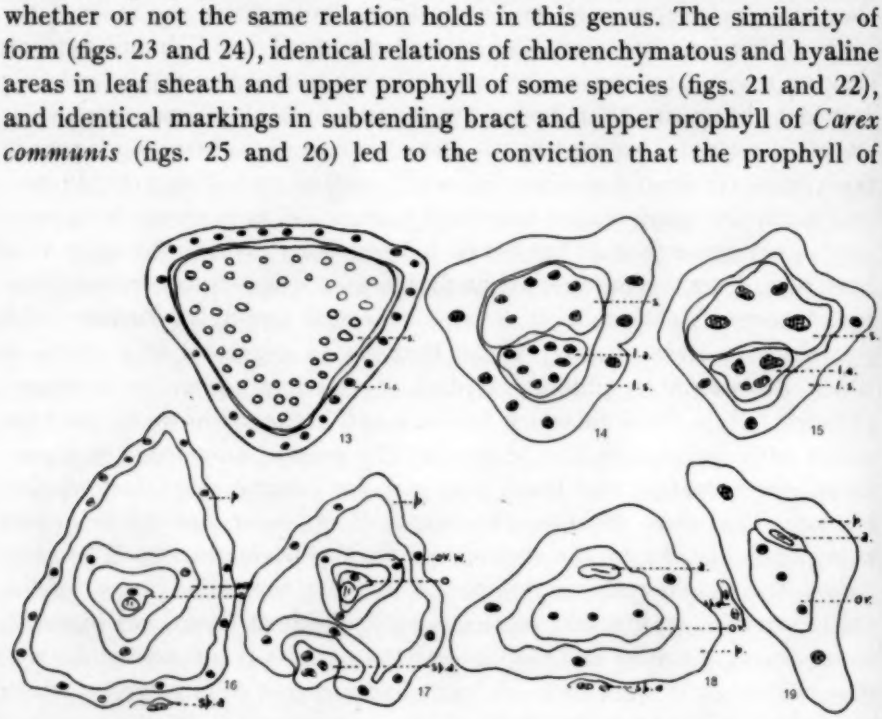
## ANATOMY OF THE PERIGYNIUM

In literature dealing with *Carex* it is around a morphological interpretation of the perigynium that early controversy developed. Does it represent one or two bracts? Is it simply an especially modified prophyll? It was with real interest that serial sections of spikelets of *Carex* were examined to get the evidence which the number, position, and course of vascular strands affords.

Because of the resemblance in the position and accompanying bicarinate condition of perigynia and pedunculate prophylls of *Carex*, an anatomical comparison of the two was attempted. It was found, however, that the pedunculate prophylls are usually entirely without vascular strands, a fact to be correlated with their delicate hyaline nature. This, in turn, is the result of their being entirely enclosed by the leaf sheath which subtends the axis to which the prophyll is attached.

Because it was observed that the prophylls of *Zebrina pendula* are

simply leaf sheaths (fig. 20) a gross comparison of leaf sheaths and pedunculate prophylls of several species of *Carex* was made to determine whether or not the same relation holds in this genus. The similarity of form (figs. 23 and 24), identical relations of chlorenchymatous and hyaline areas in leaf sheath and upper prophyll of some species (figs. 21 and 22), and identical markings in subtending bract and upper prophyll of *Carex communis* (figs. 25 and 26) led to the conviction that the prophyll of



Figs. 13–15. Cross sections of leaf sheaths of *Carex intumescens*, *C. platyphylla*, and *C. pedunculata*, respectively.

Figs. 16–19. Cross sections of perigynia of *C. intumescens*, *C. platyphylla*, *C. aurea* (abnormal), and *C. cristata*, respectively.

*a*, spikelet axis; *l. a.*, lateral axis; *l. s.*, leaf sheath; *o.*, ovule; *ov.*, ovary; *ov. w.*, ovary wall; *p.*, perigynium; *s.*, stem; *sp. a.*, spike axis.

*Carex* is usually the sheath of the first leaf of a lateral axis. It is normally bicarinate and hyaline because of its position and environment, respectively. A comparison of the vascular supply to the perigynia with that to leaf sheaths immediately suggested itself. A series of cross sections of leaf sheaths of various species of *Carex* is shown in figures 13–15. In the lower leaf sheaths of *C. intumescens* the vascular strands are numerous and distributed through a complete circumference. It will be noted that the strands are not so prominent in the thin portion of the leaf sheath opposite the midrib. Leaf sheaths of *Carex platyphylla* and *C. pedunculata* show fewer strands, all limited to that portion of the leaf sheath under the leaf blade.

An examination of the cross section of the perigynium of *C. intumescens* (fig. 16) shows a distribution of vascular strands like that in a lower leaf sheath. In *C. platyphylla* the distribution of strands in the cross section of a perigynium (fig. 17) is very much like that in a leaf sheath of the same plant. One perigynium of *C. aurea* (fig. 18) shows three vascular strands distributed like those in a leaf sheath of *C. pedunculata*. Usually in this species there are but two vascular strands running in or near the keels, as in the figured perigynium of *C. cristata* (fig. 19). The fact that, as in *C. cristata*, the perigynia of many species of *Carex* are bicarinate with a single prominent vascular strand in each keel has always been a strong argument for the origin of the perigynium of *Carex* by the fusion of two bracts. That occasionally, as in *C. aurea*, a third strand is present in the middle of the perigynium, which normally has but a strand in each keel, indicates that the perigynium of the species earlier (phylogenetically) had a midrib which has aborted. Abortion of a strand has occurred in that part of the perigynium which is crowded against the spike axis. Successive cross sections from the base of a pistillate spikelet of *C. digitalis* show abortive strands in this same region. A section near the base of the spikelet shows two strands toward the spike axis (fig. 27). A section just above shows them completely absent (fig. 28).

The vascular strands often found in the keels of a perigynium are not midrib strands of fused bracts, but they represent lateral strands of a single bract. These strands remain in regions of tissue prominence, the keels, after abortion of a midrib strand or middle strands in a region where growth is stunted by pressure of the perigynium against the axis of the spike. In the perigynia of *Carex* a reduction series exists from the many-stranded perigynia of species like *C. intumescens* and *C. platyphylla* to the two-stranded perigynia of species like *C. cristata* and the normal *C. aurea*.

The fact that the perigynium represents a single bract is further shown by its position in relation to the pistil. In the sedge family (Cyperaceae) one angle of the tricarpellate ovary (in species possessing such) is opposite the subtending bract of the flower. In those genera in which the spikes are simple, the subtending bract is attached directly to the axis of the spike (fig. 29). In species of *Carex* one angle of a tricarpellate pistil is turned toward the middle region of the perigynium, a prophyll, hence to that portion which lies against the spike axis. In other words, the orientation of the tricarpellate pistil of other genera of sedges to the subtending bract of the flower is the same as that found in tricarpellate species of *Carex*. In recognizing the perigynium as the subtending bract of the pistillate flower of *Carex*, any seeming incongruity in the position of the pistil among various genera of the Cyperaceae vanishes.

In those species of *Carex* in which the vascular strands of the perigynium are fairly numerous the midrib of the perigynium lies opposite an angle of the tricarpellate pistil (figs. 16 and 17). The fact that in some species of *Carex* there is a midrib in the perigynium opposite an angle of the tricarpellate ovary, supports the view that the perigynium represents a single bract. Such a position is entirely incompatible with the theory

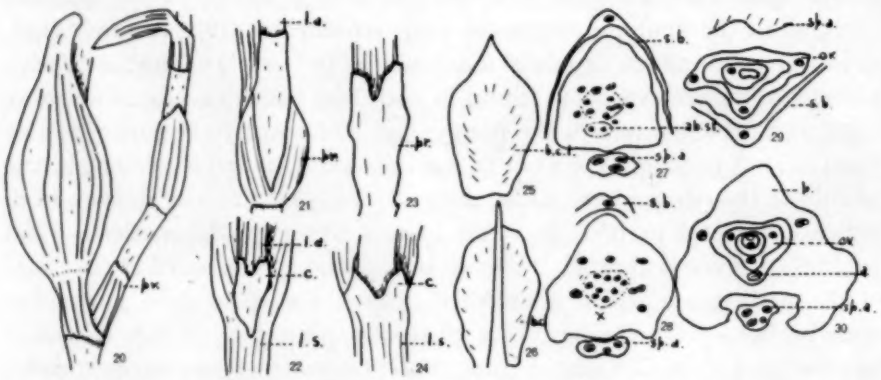


Fig. 20. Prophyll and adjacent parts of *Zebrina pendula*.

Figs. 21 and 22. Upper pedunculate prophyll and leaf sheath, respectively, of *Carex platyphylla*.

Figs. 23 and 24. Pedunculate prophyll and leaf sheath, resp., of *Carex laxiflora*.

Figs. 25 and 26. Uppermost pedunculate prophyll and opposing leaf sheath, resp., of *Carex communis*.

Figs. 27 and 28. Successive sections from the base of a pistillate spikelet of *Carex digitalis* to show abortive perigynial vascular strands.

Fig. 29. Diagram to show position of pistil in relation to subtending bract of flower in *Scirpus sp*.

Fig. 30. Cross section of base of reflexed pistillate spikelet of *Carex microglochin*.

*a.*, spikelet axis; *ab. st.*, abortive perigynial vascular strands; *b. c. l.*, brownish color line; *c.*, hyaline collar-like projection of leaf sheath; *l. a.*, lateral axis; *l. s.*, leaf sheath; *ov.*, ovary; *p.*, perigynium; *pr.*, prophyll; *s. b.*, subtending bract of pistillate spikelet or flower; *sp. a.*, spike axis.

that the perigynium represents two fused bracts. Even where a midrib is lacking, the angle of the ovary is directed toward the middle part of the perigynium which indicates that the absence of a midrib is a matter of phylogenetic abortion, an abortion correlated with its unfavorable position. A strand or strands have been lost where the development of surrounding tissues is least.

The results of an anatomical study of the perigynium clearly substantiate the view which Kunth held of the morphological nature of the perigynium. It is a single bract. It is a prophyll by position and by its bicari-

nate nature. A prophyll is the first leaf of a lateral axis; in *Carex* usually the leaf sheath only is present. When there are many vascular strands in the perigynium they show a distribution similar to that found in a leaf sheath of *Carex*. The perigynium sheaths the axis on which it is borne like a leaf sheath. Both its vascular supply and its gross morphology are that of a leaf sheath.

Because the perigynium is often bicarinate with a vascular strand in either keel (fig. 19) early workers on *Carex* thought that the perigynium represents two fused bracts and that the two strands represent midrib bundles of the bracts. In the absence of conflicting evidence these relations within the perigynium might be accepted as hinting that the perigynium has arisen in this way. But, in general, the course of vascular strands does not indicate derivation of the perigynium from two fused bracts. In many cases the vascular strands do not run in the keels of the perigynium though their course is in harmony with the position of the keels. Often the vascular strands do not even conform in their course to the keels. The explanation of this divergence seems to lie in the following facts. The keels result ontogenetically from the pressure of the perigynium against the axis of the spike. The vascular supply phylogenetically became adapted through reduction to the keeled state. Pressure disturbances or aberrations in the development of a particular spikelet would account for nonconformity between the keels of a perigynium and the course of vascular strands in the perigynium. A recent phylogenetic change in the spike habit of a particular species might account for a normal discrepancy between keels and the course of vascular strands in the perigynia of that species. Especially illuminating in this respect is the relation between the position of keels and vascular strands in spikelets of *C. microglochin*. In this species the spikelets early turn back on the parent axis (reflexed spikelets) so that the opposite side of the perigynium is appressed to the spike axis. In the cross section of the base of a spikelet (fig. 30) it will be seen that under this condition the keels are on the side of the spikelet opposite that on which they are in other species. In *C. microglochin* they are on the same side of the as the spikelet axis; in other species they are not.

Not only is the two-bract theory of the perigynium refuted by the anatomical evidence from perigynia with many strands, but it is not supported in perigynia with two strands. Sometimes keels are not even present. The keels are often not traversed by the vascular strands. The only possible support for the two-bract theory lies in the possibility that, though the keels can not be interpreted as midribs of bracts, the two vascular strands present in many perigynia represent midrib strands. There is evidence against this possibility. In occasional perigynia bearing but

a single vascular strand no other deviations from the normal are noted. If the strands actually represent the midribs of two fused bracts, one might expect to find the absence of the vascular strand accompanied by the lack of its bract, and hence, some serious malformation of the perigynium.

As has been stated in defense of the one-bract theory of the origin of the perigynium, the bicarinate nature of the perigynium is a result of its position. Pedunculate prophylls of *Carex* are bicarinate, yet these prophylls are simply leaf sheaths. Prophylls of monocotyledons, generally, are typically bicarinate but there are none which are known to have arisen by the fusion of bracts. Why the first leaf of a lateral branch of a monocotyledon should occupy the position it does against the main axis, is not known, but occupying that position, one can readily understand how pressures in the bud and in later development could make it bicarinate.

The bidentate tips of perigynia of many species of *Carex* can be correlated with the bicarinate nature of the perigynia possessing them, and should not be used as evidence for the origin of the perigynium in the fusion of two bracts. With greater development of vascular and non-vascular tissues in the keels, one can expect a tendency toward a greater terminal development of the keel regions than of the regions between. Such development has occurred in perigynia that have bidentate tips. Many perigynia terminate in an even ring of tissue.

This writer feels that the two-bract theory of the perigynium never would have had support if all the different types of perigynia had been examined. It is only the extremely reduced perigynia with prominent keels and accompanying vascular strands which even suggest the origin of the perigynium by the fusion of bracts.

In only one tricarpellate species of *Carex* was there found a significant deviation from the normal relation in position between one carpel and the middle portion of the perigynium. In *Carex pubescens* one angle of the ovary, instead of being directed toward the middle region of the perigynium, lies toward one or the other of the two perigynial strands. This orientation is fundamental; the lateral strand behaves in every respect of departure, gap formation, and orientation to flower as does the midrib of perigynia that possess such a strand. This orientation is not represented by a single abnormality, but is characteristic of the species. This peculiarity can hardly be regarded as evidence for the origin of the perigynium of *C. pubescens* in the fusion of two nearly opposite bracts. This species is but one of about fifty tricarpellate species that were investigated anatomically. The very abundance of opposing evidence moves one to regard the spikelet of *C. pubescens* as not representing a primitive condition for

the position of the pistil in relation to the perigynium. Probably the unusual orientation of pistil to perigynium in this species is of recent origin. The perigynium is of the reduced type with two lateral well developed vascular strands. It is possible, at least, that there has been a reorientation of the pistil because of the presence of the large lateral vascular strands and the absence of a midrib in the perigynium.

Probably both perigynia and prophylls of the peduncles of *Carex* have been derived phylogenetically from leaf sheaths. (There is evidence that the blade may sometimes be involved.) The trend of modification has been directed differently in the two cases. In the case of the pedunculate prophylls the trend has been toward extreme reduction and apparently toward disuse. It is difficult to ascribe any function to the hyaline slender prophylls of the peduncles. On the other hand, perigynia represent leaf sheath modification in the direction of structural and functional amplification. Perigynia are always inflated structures, often bidentate at the top, sometimes very large and richly supplied with vascular tissue. The perigynium always surrounds the ovary; and because of its early development and maturity, by comparison with the ovary itself, must offer to the latter a certain protection against water loss and mechanical injury by insects and other small animals. The perigynium protects the developing ovary in the absence of any floral protective parts. Undoubtedly perigynia aid in dissemination of the fruits of *Carex* by giving added buoyancy for transportation by water. Perigynia of various species of *Carex* can be found in some quantity on back water and pool surfaces. Even the difficulty that was experienced in exhausting air bubbles from mature and dry perigynia, in treating them preparatory to infiltration, is convincing evidence that they represent efficient floats. The distribution of various species of *Carex* along stream beds indicates the practical efficiency of the perigynia in this way.

## THE PISTILLATE FLOWER OF CAREX

Usually the pistillate flower of *Carex* is made up of three or two fused carpels though in one subgroup, *C. concinnoides* of Mackenzie, the pistil is normally composed of four fused carpels (St. John and Parker, 1925). Ovaries of the tricarpellate pistils are normally more or less triangular in cross section, whereas bicarpellate ovaries are elliptical. The ovary is always unilocular with a single, basal, anatropous ovule whose stalk is toward the axis of the spikelet.

The gross morphology of the pistillate flowers of *Carex* has long been known, but practically nothing has been written about the internal anatomy, especially the vascular structure. Yet it is the nature of the vascular

supply within the pistillate flower which may furnish the key to a proper interpretation of the phylogenetic development of the flower. Though the number of stigmas and the lobing of the ovary suggests that the pistils of *Carex* are normally either bicarpellate or tricarpellate, they should be studied anatomically to see whether the vascular supply will suggest another interpretation. The presence of a single basal ovule in a unilocular bicarpellate or tricarpellate pistil represents, according to the criteria of comparative floral morphology, an extremely reduced pistillate condition. An anatomical study of the vascular supply to the basal ovule of *Carex* should enable one to determine the type of ovule placentation from which the basal ovule, by reduction, has been derived. Perhaps it can be determined what the relation is between tricarpellate and bicarpellate pistils. Is there any vestigial vascular structure at the base of the bicarpellate pistil which would indicate its origin by reduction from the tricarpellate type of pistil?

An anatomical study of the pistillate flowers of *Carex* has been made. For the most part, the vascular supply of ovary and ovule has been involved; to a limited extent, the supply of the receptacle and of the stigmas. The vascular supply to the ovary wall and ovule has been interpreted in terms of dorsal strands (midrib strands of the component carpels) and ventral strands (marginal strands of the carpels, which normally represent the placental vascular supply). In many species of *Carex* the vascular supply of the receptacle is so confused by anastomoses of strands that one can not interpret it except in its gross features. In other species, however, the vascular supply to the parts of the simple flower can be interpreted in terms of dorsal and ventral carpel strands arising in the receptacle of the flower.

In tricarpellate pistils, for these are evidently more primitive than bicarpellate ones and hence deserve consideration first, the dorsal strands of the carpels run in the angles of the ovaries and up into the stigmas. The ventral bundles of the three carpels are never distinct, but are represented usually by three strands. These, which probably before an early (phylogenetic) fusion were six (three pairs), fuse in the receptacle of the flower to form the single ovular strand. The fact that the entire ventral supply of all the carpels making up the pistil enters the single basal ovule indicates that the immediate ancestral type of placentation for *Carex* was free central.

Baillon (1893), after ontogenetic studies, says of some bicarpellate and of some slightly abnormal tricarpellate pistils of *Carex* that what shows first of the female flower is a small hemispherical receptacle on the surface of which develop a little later two or three carpels of which one is anterior,

and that it is this latter which often remains smaller than the others and finally entirely disappears. Schumann (1890) writes of a similar condition in *Scirpus*. There is scant anatomical evidence for phylogenetic abortion of the anterior carpel. Abortive vascular tissue is found in the position which the anterior carpel would occupy if present. The detailed vascular structure of this abortive carpel is not discernible in any specimens that have been examined. (In general the vascular supply of bicarpellate pistils examined was more limited in amount and more involved than that of tricarpellate pistils.) What little anatomical evidence there is for the origin of the bicarpellate pistil harmonizes with the results of the ontogenetic bud studies of Baillon and Schumann.

## SUMMARY

1. Anatomical evidence for the morphological nature of the pistillate "flower" of *Carex* substantiates previous findings of comparative morphology and of ontogenetic studies. The pistillate "flower" of *Carex* is a spikelet bearing a single, naked, pistillate flower. The axis of the spikelet is usually abortive beyond the attachment of the pistil.

2. Primitively the spikelet was probably bisexual as it is in present day species of close relatives of *Carex*, i.e., *Kobresia* and *Schoenoxiphium*. The author has found and figured abnormal bisexual spikelets of *Carex*.

3. Normally the naked pistillate flower of the spikelet is surrounded and hidden, with the exception of the stigmas, by its subtending bract, the perigynium. The spikelet axis from the attachment of the perigynium outward is also included within the perigynium.

4. The perigynium represents a single bract, as first stated by Kunth. It is a prophyll as determined by Gay.

5. Although having certain characteristic features such as a bicarinate form, often with a vascular strand in each keel, a prophyll is the first leaf of a lateral axis. Usually only the sheath of this leaf is present in *Carex*, as in *Zebrina pendula*.

6. The perigynium thus usually represents the sheath of the first leaf of a lateral axis. The fact that it is a leaf sheath, readily accounts for the way in which it includes the axillary pistillate flower and the end of the axis.

7. Statement 6 of this summary is substantiated by the fact that the vascular supply of perigynia with many strands is like that of leaf sheaths of *Carex*. A reductional series from many-stranded perigynia to those with only two strands exists, showing that the latter represent the product of a phylogenetic vascular modification.

8. Excellent confirmatory evidence for the statements of sections 3, 4, and 5 of this summary is seen in the position of a tricarpellate pistil of

*Carex* in relation to the perigynium. One angle of the ovary lies opposite the midrib of the perigynium if a midrib is present, and always, with one exception noted by the author, opposite the middle region of the perigynium. This corresponds to the condition in other genera of the Cyperaceae, where one angle of the ovary lies opposite the midrib of the subtending bract of the flower.

9. In the compound pistils of *Carex*, *Uncinia*, and *Kobresia*, and presumably in all the genera of the Cyperaceae, the dorsal bundles, that is, the midribs of the carpels, run unbranched through the ovary to enter the stigmas. In most cases the ventral bundles of a carpel do not exist separately but as a single bundle, because of phylogenetically earlier fusion; rarely they may be separate. The two or three ventral fusion bundles all fuse together in the receptacle of the flower to form the vascular strand which runs into the single, basal, anatropous ovule.

10. The ovule is always single, basal, and anatropous. Because of its constant singleness and basal position and because of the nature of its vascular supply (outlined in section 9 of this summary), it seems certain that the ovule represents the limit of reduction from several ovules and free central placentation.

11. Although anatomical evidence for the phylogenetic abortion of the anterior carpel of a tricarpellate pistil to form the bicarpellate pistil of many species of *Carex* is meager, it does confirm the positive ontogenetic evidence of Payer and Schumann.

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